DESCRIPTIONS OF *LATHROPATUS NEMORUM*, GEN. ET SP. NOV., AND SIX NEW *OOPERIPATUS* DENDY (ONYCHOPHORA : PERIPATOPSIDAE) FROM SOUTH-EASTERN AUSTRALIA

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A new genus and species, *Lathropatus nemorum* (Onychophora : Peripatopsidae), from near Portland in western Victoria is described. This is the first time an ovoviviparous onychophoran has been recorded from Victoria. Six new *Ooperipatus* Dendy, 1900 from south-eastern New South Wales and Victoria are described: *O. birrgus*, sp. nov.; *O. caesius*, sp. nov.; *O. lepidus*, sp. nov.; *O. nebulosus*, sp. nov.; *O. porcatus*, sp. nov.; and *O. silvanus*, sp. nov.—more than doubling the number of nominal species in the genus. A table of diagnostic characters for all *Ooperipatus* is provided to assist with species identification.

Key words: Onychophora, *Lathropatus*, *Ooperipatus*, Australia, new taxa.

THE PRESENT study follows from a previous review of Australian Onychophora (Reid 1996). That study was based largely on preserved museum specimens. Those from south-eastern Australia were poorly represented in collections, so recent work has concentrated on collecting and describing new species from this region.

The current study focuses on *Ooperipatus* Dendy, 1900: one of thirteen genera of Australian Onychophora that comprise, or include, oviparous species. Arthur Dendy's discovery of the first oviparous onychophoran, *Ooperipatus oviparus* (Dendy, 1895), was a dramatic affair that resulted in much scientific controversy. Tait et al. (1990) provide a colorful review of this historical event.

Ooperipatus is widespread throughout south-eastern Australia. Various species from the following genera are known to occur with *Ooperipatus*: *Euperipatoides* Ruhberg, 1985; *Ooperipatellus* Ruhberg, 1985; *Planipapillus* Reid, 1996 and *Ruhbergia* Reid, 1996. They are found from the southern highlands at altitudes up to approximately 1600 m, to the eucalypt forests of the adjacent escarpment in the south-eastern corner of the country.

Monophyly for *Ooperipatus* has not yet been demonstrated. In a phylogenetic analysis that included 62 peripatopsids, all four nominal *Ooperipatus* were part of a large unresolved clade that included 31 other taxa (Reid 1996). Within this large group, *O. oviparus* and *O. centunculus* Reid, 1996 formed a clade supported by only two unambiguous synapomorphies, but *O. hispidus* Reid, 1996 and *O. pulchellus* Reid, 1996 were not part of this monophyletic group. The lack of clear resolution in this analysis may be a reflection of the close morphological similarity among many peripatopsids (and *Ooperipatus* in particular) making such analyses of relationships based on morphological characters very difficult, or, it could be that *Ooperipatus* is para- or polyphyletic. No attempt has been made in the present study to answer this question.

A representative of a new genus and species, *Lathropatus nemorum*, from near Portland in western Victoria is also described below. This is the first record of an ovoviviparous onychophoran from Victoria.

MATERIALS AND METHODS

Specimen collection and preservation

This study is based on the examination of preserved specimens, most of which were hand collected from within and under decomposing logs. Specimens were preserved partially following the method of Reid (1996). Animals were anaesthetised by exposure to ethyl acetate vapour for 10 minutes; dipped in 70% ethanol to render the cuticle less hydrophobic; fixed in 4% formalin for 2–3 days; then stored in 70% ethanol. Animals preserved in this way are distended, enabling characters to be examined more easily than is possible in contracted specimens.

Tissue preparation for transmitted light microscopy

Cuticular tissue was cleared in a small volume (approx. 1 ml) of saturated potassium hydroxide (KOH/H_2O) solution on a hotplate set at approximately 50°C. Following clearing (approx. 1 h; tissue appears translucent), a drop of 1% aqueous aniline blue was added with sufficient lactic acid (approx. 2 drops) to neutralise the solution, rendering the aniline blue the correct color for staining. [In extreme alkaline conditions (KOH/H_2O solution) aniline blue appears red; neutralising the solution, or making it slightly acidic, restores the blue color of the stain.] Tissue pieces were stained for 15 minutes, rinsed in water and mounted in glycerol jelly. The stained and mounted tissue was examined using a compound microscope and drawings made using a camera lucida.

This method differs slightly from that of Reid (1996). Washing tissue pieces after clearing, as detailed in Reid (1996), has proved very difficult (cleared tissue pieces are often difficult to see, and consequently so often lost during washing) and time consuming, so this step has been eliminated from the method.

For males and females of each species, the following tissue samples were prepared as above: dorsal integument; nephridioporcs; crural papillae (where present) from oncopods 3 (or 2), 7 (or 8) and 12; anterior accessory gland papillae and the area surrounding the posterior accessory gland foramen.

Tissue preparation for scanning electron microscopy

Tissue dissected from fixed and preserved specimens was dehydrated in a graded ethanol series. Following three washes in 100% ethanol, tissue pieces were impregnated in hexamethyldisilazane (HMDS) by taking them through a graded ethanol/HMDS series to 100% HMDS, air dried and gold coated. Each step in the dehydration series was 5 minutes. Specimens were examined in a Philips 505 scanning electron microscope operated at 20.1 kv.

Terminology

Terminology for all characters follows Reid (1996). Head width is used as an indicator of size as this measure is less prone to variation due to the degree of distension of the body than are other size indicators such as total length. Where measurements and counts are given, these refer only to type specimens (except in the case of *O. silvanus*, sp. nov., in which some non-type specimens were measured in addition to the types). Measurement values are expressed as minimum–mean–maximum. The anterior accessory glands are described as short if they do not extend anteriorly beyond the level of oncopod 14, and long if they extend anteriorly beyond oncopod 14.

Abbreviations

Ck	Creek
E	east
EDI	eye diameter index (eye diameter expressed as a proportion of head width)
HWE	width of head measured dorsally between the midpoint of each eye
Hwy	Highway
juv.	juvenile
km	kilometres
m	metres
mm	millimetres
Mt	Mount
MV	Museum Victoria, Melbourne
N	north
NP	National Park
NW	north-west
Rd	Road
S	south
SAM	South Australian Museum, Adelaide
Tk	Track

TAXONOMY

Morphological variation within and among populations was assessed to identify species.

Species descriptions were generated by using the DELTA (Description Language for Taxonomy) software system (Dallwitz 1980; Partridge et al. 1993; Dallwitz et al. 1993).

Lathropatus, gen. nov.

Type species. Lathropatus nemorum, sp. nov., by monotypy.

Diagnosis

Both sexes lack modified head papillae. Distal papillar scales ribbed proximally, not ribbed distally, papillose in both sexes. Smooth region surrounding crural papillae foramen narrow, ovoid or lip-shaped, not extending to papillar margin. Fifteen oncopod pairs. Male crural papillae on oncopods 2–14. Ovoviviparous, ova yolky, follicular.

Etymology

The generic name, *Lathropatus*, is derived from the Greek *lathrios*, meaning 'secret', or 'hidden', and *peripatos*, or 'walking' (from which is derived the common name for Onychophora, family, and some generic names). Gender masculine.

Lathropatus nemorum, sp. nov.

Figs 1A–E; 2A–E; 3A–G; 4A–D; 5A, B

Material examined

Holotype. ♂, Victoria, Cobboboonee State Forest (southern end), approx. 11.4 km NW of Portland, beside Elbow Rd, off Nelson Portland Rd, 1.3 km N of intersection of Elbow Rd and Nelson Portland Rd, 38°17′S,141°33′E, 60 m, 26.ii.2000, coll. A. Reid and R. Roberts (MV K-7314).

Paratypes. Victoria: 4♂, 7♀, data as for holotype (MV K-7315).

Other material examined. Victoria: 6♂, 14♀, Cobboboonee State Forest (northern end), beside T and W Rd, 3.9 km S of intersection of Princess Hwy and T and W Rd, 38°02′S,141°26′E, 120 m, 27.ii.2000, coll. A. Reid and R. Roberts (MV).

Description

Measurements. HWE males 0.85–0.92–1.05 (n = 5, holotype 0.95 mm HWE); females 1.02–1.06–1.25 (n = 7).

Color pattern. Body pigmented; pigment not soluble in alcohol. Body patterned; ground-color tan, brown, olive green, or greyish-blue; primary papillae light-colored basally, dark tipped. Mid-

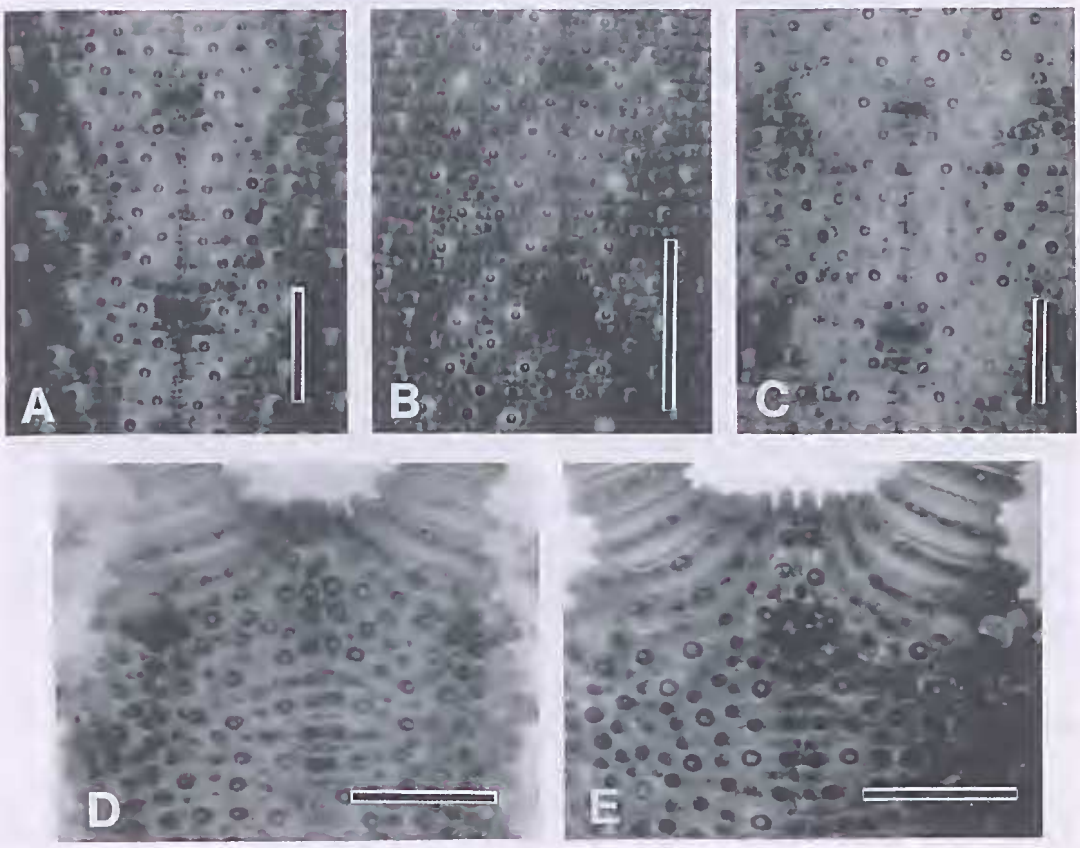


Fig. 1. Lathropatus nemorum, gen. et sp. nov.: A, body, dorsal view, holotype male, 0.95 mm HWE, scale bar 0.50 mm. B, body, dorsal view, paratype female, 1.12 mm HWE, scale bar 1 mm. C, body, dorsal view, paratype male, 1.05 mm HWE, scale bar 0.50 mm. D, head, holotype male, 0.95 mm HWE, scale bar 0.40 mm. E, head, paratype female, 1.25 mm HWE, scale bar 0.50 mm.

dorsal dark stripe present, or absent; 1–3 dark brown or black (median pair darkest) papillae on each side of dorsal midline forming distinct patch dorsal to each oncopod pair (Fig. 1A–C): broad longitudinal light ground colored band on each side of midline, band expanded dorsal to each oncopod pair forming semicircular patches (in 9 of 12 type specimens); light-colored band in tan specimen bordered by black band extending to base of oncopods (Fig. 1C); laterally with longitudinal light-colored band dorsal to oncopods. Oncopods similar color to, or slightly paler than, body; with tan or cream colored patches at junction with feet. Ventral organs white or cream. Newborn animals not pigmented.

Papillae around anal opening pigmented as for rest of body. Ventral pigment present; ventral organs white, grey patches extending from ventral organs to base of oncopods. Spinous pads pale yellow, or tan. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally (8 of 12 type specimens), or not banded, tan dorsally, grey-blue ventrally (4 of 12 type specimens); dorsal banding on proximal half of each antennal ring (distal half ground-color), with every fourth ring predominantly tan. Approximately 30 antennal rings in adults and juveniles; wide and narrower antennal rings alternate; single row of bristles on each antennal ring. Distal 8–9 antennal rings with sensory bulbs. Proximal antennal rings expanded ventrally to form sensory pads with up to two rows of sensilla with sensory bristles.

Eyes. Present. EDI males 0.08–0.09–0.10; females 0.07–0.09–0.10.

Head (males). Males with no modification of head papillae (Figs 1D; 2A, B) (ie. papillae on head do not differ significantly from remaining dorsal papillae). Head papillae with ribbed scales (Fig. 2B).

Head (females). Females with no modification of head papillae (Fig. 1E).

Jaws. Inner jaw with 5–6 denticles. Diastema on inner jaw absent; outer jaw with accessory tooth. Tongue with a longituudianl row of 6–7 teeth. Buccal folds in a single unbroken row.

Integument. Dorsum with 12 complete plicae between oncopods; wide and narrower plical folds alternate. Papillae arrangement: primary papilla with short, narrow bristle between pair of larger primary papillae with longer, more robust bristles and smaller secondary papilla(e) between primary papillae (Fig. 1A–C); conical apical piece absent; remaining integument with low scales. Males with 11–13–15, females with 11–16–20 papillae counted from the mid-dorsal line to the junction of oncopod 10. Dorsal body papillae not uniform size; alternate plicae with markedly larger primary papillae; dorsal primary papillae semicircular, or cylindrical; papillar scales ribbed proximally (microcristae well defined), not ribbed distally (microcristae fused) (Figs 2C, D; 3A, B), papillose distally in both sexes (Fig. 2C, D); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body; papillae around anal opening slightly larger than those on rest of body.

Oncopods. Number invariant intraspecifically; 15 pairs in both sexes. First pair of oncopod feet not enlarged, similar in size to remaining feet. Last pair of oncopods in both sexes well developed, not reduced, orientation as for remaining oncopods. Basal foot papillae absent; distal foot papillae present, one anterior, one median, one posterior, each with single sensory bristle. With three complete spinous pads; fourth broken spinous pad present. Spinous pads well-developed on all oncopods. Nephridiopores at centre of third spinous pad on fourth and fifth oncopod pairs, with U-shaped foramen and smooth, ovoid margin (Figs 2E; 3C).

Male reproductive tract. Gonopore between last pair of oncopods; male genital pad pad low, semicircular; slightly protruding, papillae with ribbed scales; gonopore cruciform (transverse arms longest). Vasa efferentia with thin flexible walls; proximal vasa efferentia not markedly broad; lying close together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from vasa efferentia for short distance before looping posteriorly toward gonopore (Fig. 3D), not thick walled, opaque, not shiny. Spermatophore pouch present.

Male glands and gland papillae. Crural glands, one per oncopod. Crural papillae, one per oncopod present on ventral side of oncopods 2–14; protrude between plicae 5–6 (counting from third spinous pad). Papillae similar in shape on all oncopods: semicircular proximally, tapered abruptly, semicircular or cylindrical distally; with finely ribbed scales basally, distally scales with distinct ribs;

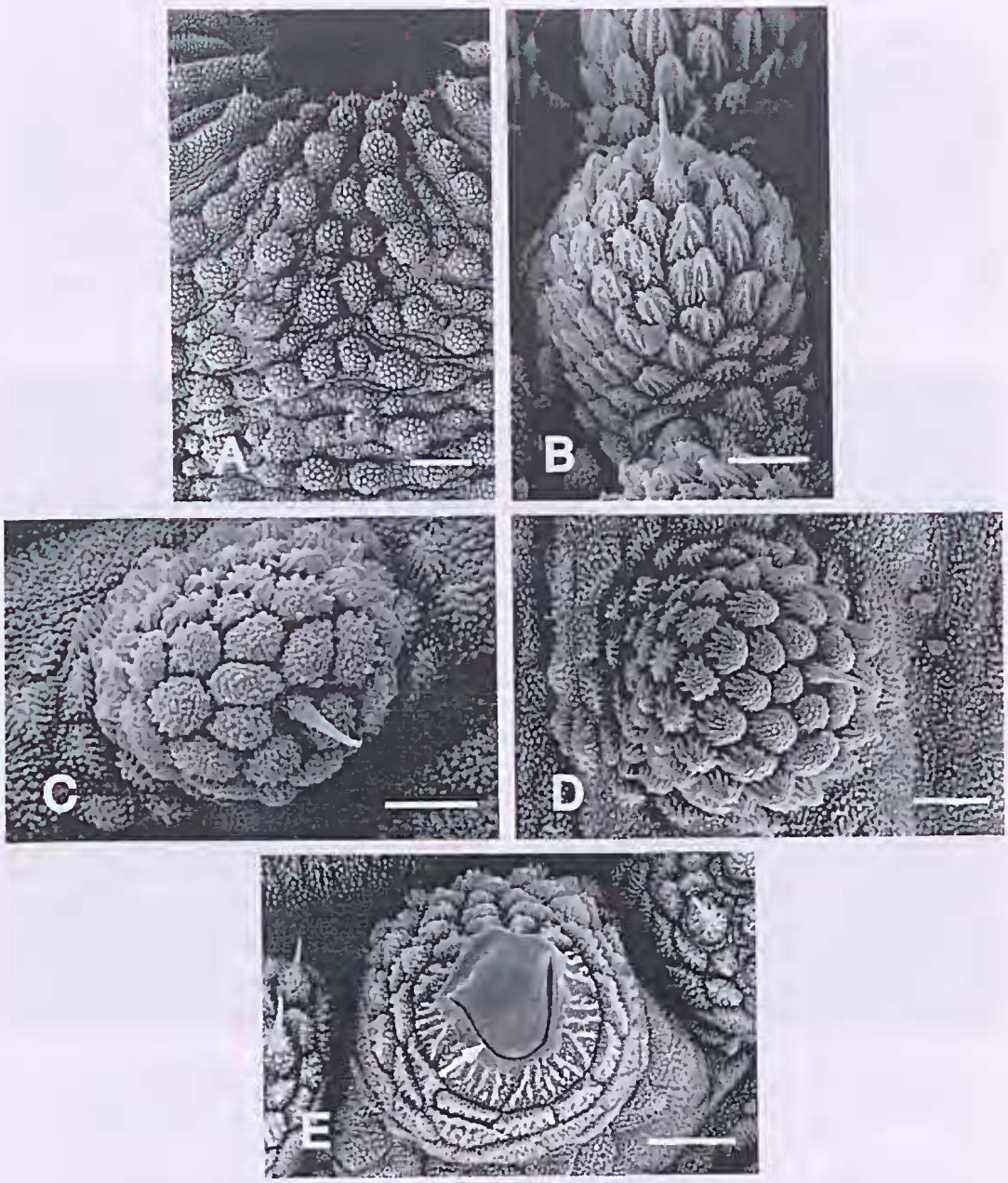
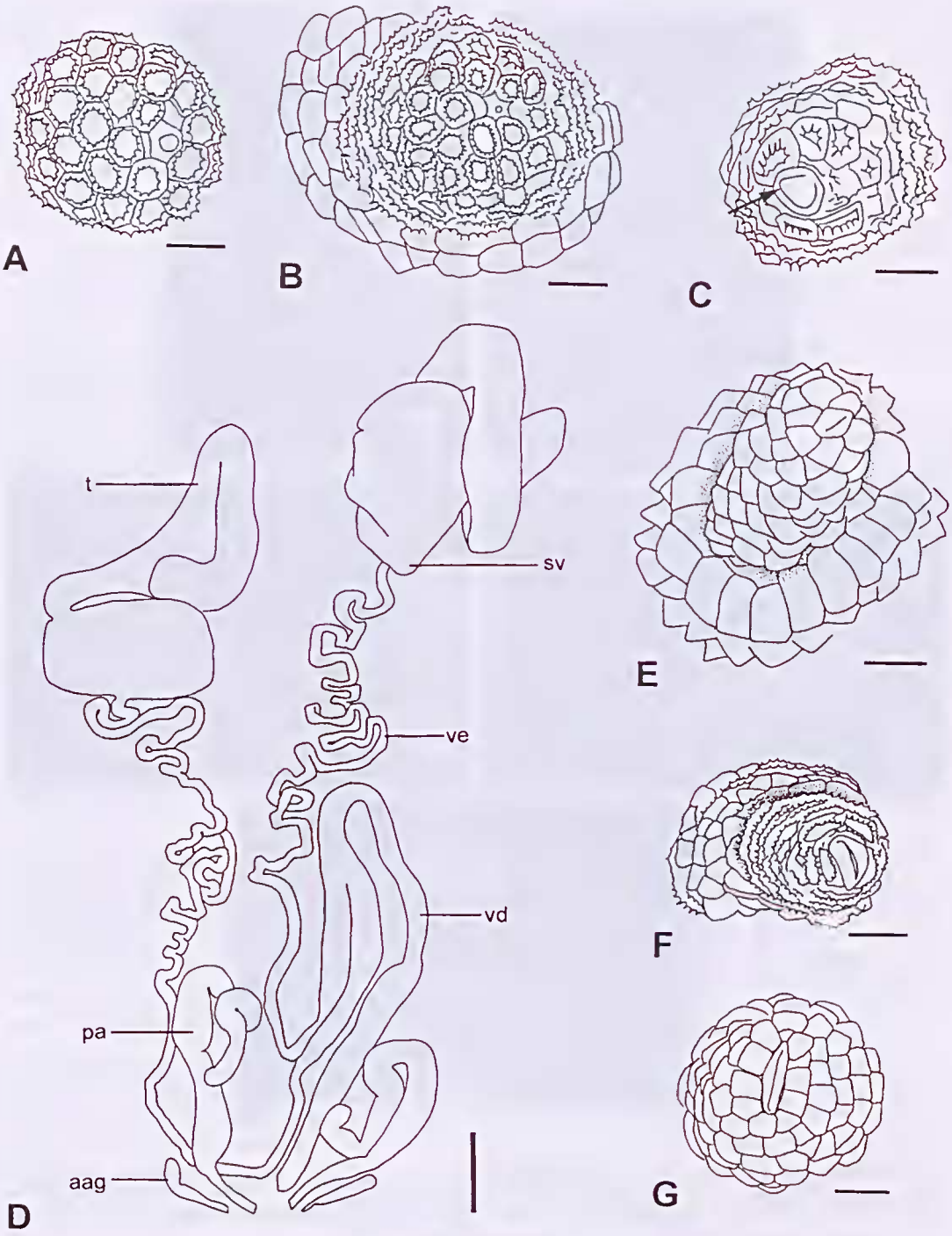


Fig. 2. Lathropatus nemorum, gen. et sp. nov., scanning electron micrographs: A, anterior portion of head, dorsal view, scale bar 100 μm. B, primary papilla, head. C, primary papilla, body. D, primary papilla, body, paratype female, 1.05 mm HWE. E, nephridiopore, oncopod 5 (arrow indicates U-shaped foramen), scale bar 40 μm A–C, E, paratype male 0.87 mm HWE. B–D, scale bars 20 μm.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smooth region surrounding distal foramen ovoid (median oncopod pairs) (Figs 3E; 4B) or lip-shaped (anterior and posterior oncopod pairs) (Figs 4A, C; 3F), not extending to papillar margin. Crural glands do not extend into lateral haemocoel, confined to oncopods. Coxal organs absent. Anterior accessory gland papillae present; open on genital segment at base of last pair of oncopods; without smooth distal region; semicircular; foramen a longitudinal slit (Figs 3G; 4D). Anterior accessory glands present; short (Fig. 3D); lying freely within perivisceral haemocoel; extending anteriorly approximately to oncopod 14; contents opaque white or cream. Posterior accessory glands present; open approximately midway between genital and anal openings; gland foramen separate, close together; glands broad and saccate; folded distally, long hook tapered only slightly to blunt tip (Fig. 3D).

Female reproductive tract. Females without ovipositor; ovoviviparous; gonopore foramen shape cruciform (with arms equidistant). Ovarian tubes separate, suspended along entire length to pericardial floor; with thin walls; oviduets unite close to ovary. Spermathecae open into oviduct via single duet. Receptaculum ovorum absent. Additional pouches present. Embryos in individual uteri at successive stages of development along length of uteri (female specimens from both collection sites contained well-developed embryos in the uteri).

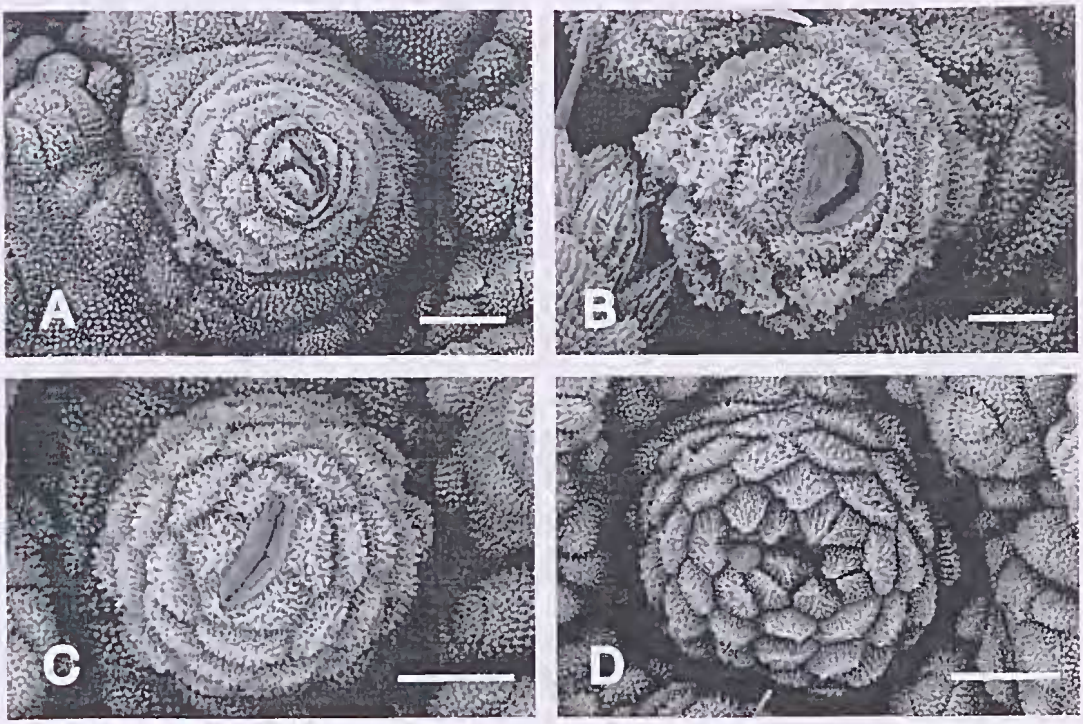


Fig. 4. Lathropatus nemorum, gen. et sp. nov., scanning electron micrographs: A, crural papilla oncopod 4. B, crural papilla oncopod 7. C, crural papilla oncopod 12. D, anterior accessory gland papilla. A–D, paratype male 0.87 mm HWE. Scale bars 20 μm.

Fig. 3. Lathropatus nemorum, gen. et sp. nov.: A, primary papilla, paratype male, 0.87 mm HWE, scale bar 0.02 mm. B, primary papilla, paratype female, 1.05 mm HWE, scale bar 0.02 mm. C, nephridiopore oncopod 4, paratype male, 0.87 mm HWE, scale bar 0.02 mm (arrow indicates U-shaped foramen. D, male reproductive tract and associated glands, paratype, 0.87 mm HWE, scale bar 0.50 mm (aag, anterior accessory gland; pa, posterior accessory gland; sv, seminal vesicle; t, testis; vd, vas deferens; ve, vas efferens). E, crural papilla oncopod 8, paratype male, 1.05 mm HWE, scale bar 0.02 mm. F, crural papilla oncopod 12, paratype male, 0.87 mm HWE, scale bar 0.02 mm. G, anterior accessory gland papilla, paratype male, 0.87 mm HWE, scale bar 0.02 mm.

Character	*Anoplokaros*	*Euperipatoides*	*Lathropatus*	*Mantonipatus*	*Occiperipatoides*	*Tasmanipatus*
Body pigmented (pig.)/ patterned (pat.)	pig./pat.	pig./not pat. (some scattered tan papillae, but no distinct pattern)	pig./pat.	pig./pat.	pig./pat. or not pat.	pig. or not pig./not pat.
Antennal ring No.	30	> 30	30	30	30	> 30
Rows of bristles on distal antennal rings	1	2	1	1	2	2
Male distal papillar scales	ribs partially fused	ribbed	ribs partially fused	ribbed	ribbed	ribbed
Female distal papillar scales	ribs partially fused	ribbed	ribs partially fused	ribbed	ribbed	ribbed
Basal foot papillae	A	A	A	A	A	P
Vas deferens relative length*/wall thickness	short/thin, opaque	short/thin, opaque	short/thin, opaque	short/thin, opaque	short/thin, opaque	long/thick, shiny
Oncopods with crural papillae	2–14	2–14	2–14	11–14	1–14 or 15	6–14
Smooth region surrounding crural papillae foramen	extends around papillar margin (Fig. 5A–C)	narrow, ovoid, or lip-shaped	ovoid or lip-shaped (Fig. 4A–C)	wide, ovoid, extending to papillar margin	wide, ovoid, extending to papillar margin, or around papillar margin	wide, ovoid, extending to papillar margin (*T. anophthalmus*) or lip-shaped (*T. barretti*)
Crural glands	confined within oncopods	confined within oncopods	confined within oncopods	extend from oncopods 12–13 into haemocoel	extend from oncopods 1 into haemocoel	confined within oncopods, or extend from oncopods 6–12 into haemocoel
Anterior accessory glands	short	long	short	long	long	long

Table 1. Comparison of selected characters of six peripatopsid genera: Australian ovoviviparous genera which lack modified head papillae in males. A = absent; P = present. *In some onychophorans the vas deferens continues anteriorly for a short distance only, or loops posteriorly immediately following the junction of the paired vasa efferentia (here called 'short'); in others the vas deferens continues anteriorly for a considerable distance before looping posteriorly toward the gonopore ('long').

Female glands and gland papillae. Crural papillae absent. Additional opening in females, posterior to gonopore (as seen in *Tetrameraden meringos* Reid, 1996) absent; glands associated with posterior reproductive tract absent.

Remarks

Most non-type specimens (*Other material examined*) lack the distinct, dark mid-dorsal patches which are present in the type material. The light-colored semicircular patches on each side of the midline are indistinct, or absent in very dark specimens (Fig. 1B).

Given the propensity in Onychophora toward cryptic speciation and the narrow distributional range occupied by many species, the specimens listed in the *Other material examined* section above, found approximately 30 km from the type locality are assigned only tentatively to *L. nemorum*. While some minor differences have been noted above, genetic techniques will undoubtedly need to be applied to clarify possible species boundaries.

This new species is one among relatively few nominal Australian taxa that lack male modified head papillae. Two of these, *Ooperipatellus* and *Ooperipatus* (some species only), are oviparous, so clearly differ from this new taxon. In addition, *Ooperipatellus* have 14, rather than 15 oncopod pairs and a very different male reproductive tract (see Reid 1996: fig. 100). Of those remaining (*Anoplokaros* Reid, 1996; *Euperipatoides*; *Mantonipatus* Ruhberg, 1985; *Occiperipatoides* Ruhberg, 1985; and *Tasmanipatus* Ruhberg et al., 1991), this species is most similar to *Anoplokaros keerensis* Reid, 1996 from eastern New South Wales. Differences between *Lathropatus* and the five genera listed above are summarised in Table 1.

Lathropatus nemorum and *A. keerensis* differ in two main character states:

i. The smooth rims surrounding the foramen of the crural papillae on oncopods 11–14 extend around the papillar margin in *A. keerensis*, but are narrow, ovoid, or lip-shaped in *L. nemorum* and do not extend to the papillar margin.

ii. While lacking an obvious head structure, or modified head papillae, a number of *A. keerensis* specimens were found to have some irregularities in the mediodorsal head papillae (Reid 1996). These papillae may be enlarged or irregular in outline. While not of significant magnitude and not clear on all specimens, this observation led Reid (1996: 732) to suggest that, 'it is possible that a head structure may have been lost in this species'. The phylogenetic analysis (Reid 1996: fig. 27) lent further support to this hypothesis. *Anoplokaros keerensis* was shown to be part of a clade with *Reginitra quadricanla*, a species with an elaborate head structure. The reconstructed ancestral state for the character 'modified head papillae or structure anterior to eyes', was found to be equivocal. The ancestor of these two species may, or may not have had a head structure.

In contrast, no trace of a head structure, or indication of modified head papillae can be seen in *L. nemorum*. The papillae on the heads of male *L. nemorum* are regular in outline (Fig. 2A) and the papillar scales are directed toward the sensory bristles of the papillae (Fig. 2B). Those of *A. keerensis* are slightly irregular in outline, and the papillar scales project slightly outwards from the central bristles, giving them a spiny appearance.

Other minor differences between the two taxa, *A. nemorum* and *A. keerensis*, are: the papillae surrounding the anal opening in *A. keerensis* are tan, while those in *L. nemorum* are the same color as the rest of the body, and each antennal ring is tan-banded in *L. nemorum*, while only alternate rings are banded in *A. keerensis*.

On the weight of available evidence, there is greater support for the erection of a new genus, for this newly discovered taxon than its inclusion within the genus *Anoplokaros*. It would not be surprising to find, however, that when other, perhaps molecular, characters are examined, the two genera may be found to be closely related.

Habitat

All type specimens were found in decomposing logs in dry sclerophyll forest. Cobboboonce State Forest has four main eucalypt species: *Eucalyptus obliqua* (messmate stringybark), *E. baxteri* (brown stringybark), *E. viminalis* (manna gum) and *E. willisii* (narrow-leaf peppermint). The non-type specimens were all found (within a very short space of time) in and under logs in a pine plantation. Given the amount of decomposing timber pieces on the ground, it is likely that many hundreds of specimens probably occur in this plantation. Hand collected specimens were usually found lying flat, with anterior half of body curved and the head partially tucked in loop of body.

Distribution

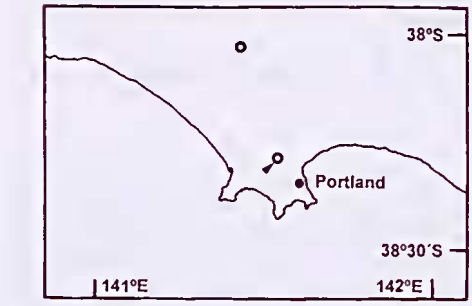
Victoria, Cobboboonce State Forest 38°02′S, 141°26′E–38°17′S,141°33′E (Fig. 5).

Etymology

The specific name, *nemorum*, is derived from the Greek, *nemos*, meaning 'forest' or 'wood'.

Genus *Ooperipatus* Dendy

Ooperipatus Dendy, 1900: 509–511.



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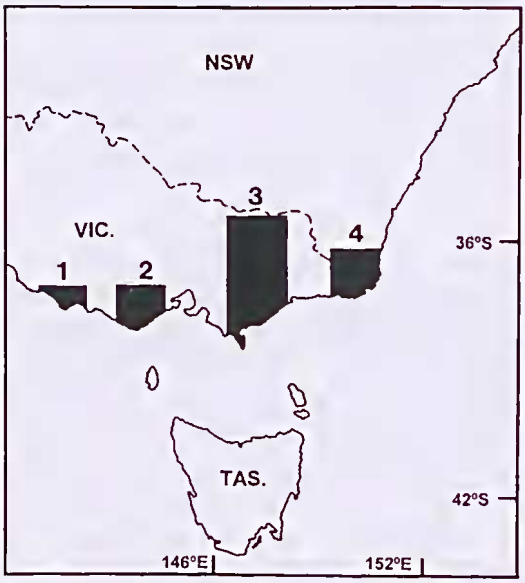


B

Fig. 5. A, *Lathropatus nemorum*, gen. et sp. nov., collection sites (open circles), arrow indicates type locality. B, section of south-eastern Australia showing regions illustrated in detailed distribution maps: 1, area enlarged in A above; 2, area enlarged in Fig. 17; 3, area enlarged in Fig. 10; 4, area enlarged in Fig. 8.

Type species. Peripatus oviparus Dendy, 1895, by monotypy.

Diagnosis (emended)

Males with or without modified papillae on head. Modified papillae, when present, fused forming ridges with scales projecting outwards, or not fused, papillar scales project outwards from central bristle, appear spiny. Fifteen oncopod pairs. Oviparous, ova follicular.

Description

This generic description comprises characters present in all *Ooperipatus* species. Only characters that differ among species are given in the species descriptions to follow.

Color pattern. Body pigmented; pigment not soluble in alcohol. Body patterned. Mid-dorsal dark stripe absent. Color of oncopods similar to, or slightly paler than, body; with light-colored patches at junction with feet. Ventral organs white or cream.

Antennal rings. Proximal antennal rings expanded ventrally to form sensory pads; sensilla with sensory bristles.

Eyes. Present.

Head (males). Eversible head structure absent. No shallow furrow on head between antennae.

Jaws. Inner jaw with 4–6 denticles. Diastema on inner jaw absent; outer jaw with accessory tooth. Tongue with longitudinal row of 5–7 teeth. Buccal folds in single unbroken row.

Integument. Dorsum with 12 complete plicae between oncopods; wide and narrower plical folds alternate. Papillae arrangement: primary papilla with short, narrow bristle between pair of larger primary papillae with longer, more robust bristles and smaller secondary papilla(e) between primary papillae; conical apical piece absent; remaining integument with small scales; papillae around anal opening slightly larger than those on rest of body.

Oncopods. Number invariant intraspecifically; 15 pairs in both sexes. First pair of oncopod feet not enlarged, similar in size to remaining feet. Last pair of oncopods in both sexes fully developed; orientation as for remaining oncopods. Basal foot papillae absent; distal foot papillae present, one anterior, one median, one posterior. With three

complete spinous pads; fourth broken spinous pad present. Spinous pads well-developed on all oneopods. Nephridiopores at centre of third spinous pad on fourth and fifth oneopod pairs.

Male reproductive tract. Gonopore between last pair of oneopods; male genital pad low, semi-eireular; slightly protruding, papillae with ribbed seales; gonopore a longitudinal slit, extending elose to rim of genital pad. Vasa efferentia with thin flexible walls; proximal vasa efferentia not markedly broad; vas deferens not thick walled, opaque, not shiny. Spermatophore poueh present.

Male glands and gland papillae. Crural glands, one per oneopod. Crural papillae open via short slit. Some erural glands extend into lateral haemoeoel. Coxal organs absent. Anterior accessory gland papillae present; open on genital segment at base of last pair of oneopods; without smooth distal region. Anterior aecessory glands present. Posterior aceessory glands present; open direetly to exterior externally on anal segment; glands broad and saeeate.

Female reproductive tract. Female with ovipositor; oviparous; gonopore foramen shape a longitudinal slit. Ovarian tubes separate, suspended along entire length to pericardial floor; with thin walls; oviduets unite elose to ovary. Ova follieular; large, yolky. Spermatheeae open into oviduct via single duet. Reeeptaculum ovorum absent. Additional pouehes present.

Female glands and gland papillae. Crural papillae absent. Additional opening in females, posterior to gonopore (as seen in *Tetrameraden meringos* Reid, 1996) absent; glands associated with posterior reproduetive traet absent.

Remarks

The generie diagnosis has been modified from Reid (1996: 829) to include the words 'or without' with respeet to the male modified head papillae. Two new speeies, *O. caesius*, sp. nov. and *O. silvanus*, sp. nov., do not have modified head papillae in males, but elearly eonform to *Ooperipatus* in all other respeets, so the generie diagnosis has been modified aeeordingly.

The only other oviparous speeies that lack any modifieation of the male head or head papillae belong to the genus *Ooperipatellus* Ruhberg, 1985. Members of this genus have fourteen, rather than fifteen oneopod pairs, and the male reproductive traet of *Ooperipatus* differs signifieantly from that of *Ooperipatellus*: there is little ehanee that members of these two genera could be eonfused.

Ooperipatus birrgus, sp. nov.

Figs 5B; 6A–C; 7A–H; 8

Material examined

Holotype. ♂, NSW, South East Forests NP, Coolangubra Section, 5 km N of intersection of Coolangubra Forest Way and Northern Access Rd, 37°01′S,149°23′E, 800 m, 2.ii.1999, coll. A. Reid (MV K-7316).

Paratypes. NSW: 1♂, 1♀, data as for holotype (MV K-7317).

Diagnosis

Antennae banded on the proximal half of eaeh antennal ring. Males with a patch of spiky papillae on head anterior to eyes. Crural glands present on oneopods 1–14; erural papillae similar in shape on all oneopods: semieireular or eylindrieal distally, not pointed; erural glands extending into lateral haemoeoel long, often folded baek along length.

Measurements. HWE males 1.15–1.28–1.42 mm (n = 2, holotype 1.42 mm HWE); female 1.90 mm (n = 1).

Color pattern (Fig. 6A, B). Ground-eolor tan, olive green, or brown; primary papillae unieolorous, or light-colored basally, dark tipped (largest primary papillae light basally, dark brown distally in all speeimens). Pair of dark brown papillae dorsal to eaeh oneopod, one eaeh side of mid-dorsal line (males only); series of joined diamonds along midline, lateral angles in line with oneopods (ean appear sealloped in fully distended speeimens); diamonds lighter-colored than surrounding integ-ument and usually bordered by darker pigment; laterally with longitudinal light-eolored band dorsal to oneopods, or with light-colored patehes between oneopods. Papillae around anal opening pigmented as for rest of body. Ventral pigment present and very pale; with dark patches extending from oneopods to ventral organs. Spinous pads tan, or grey. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally (trace ventrally); dorsal banding on proximal half of eaeh antennal ring (distal half ground-eolor). Greater than 30 antennal

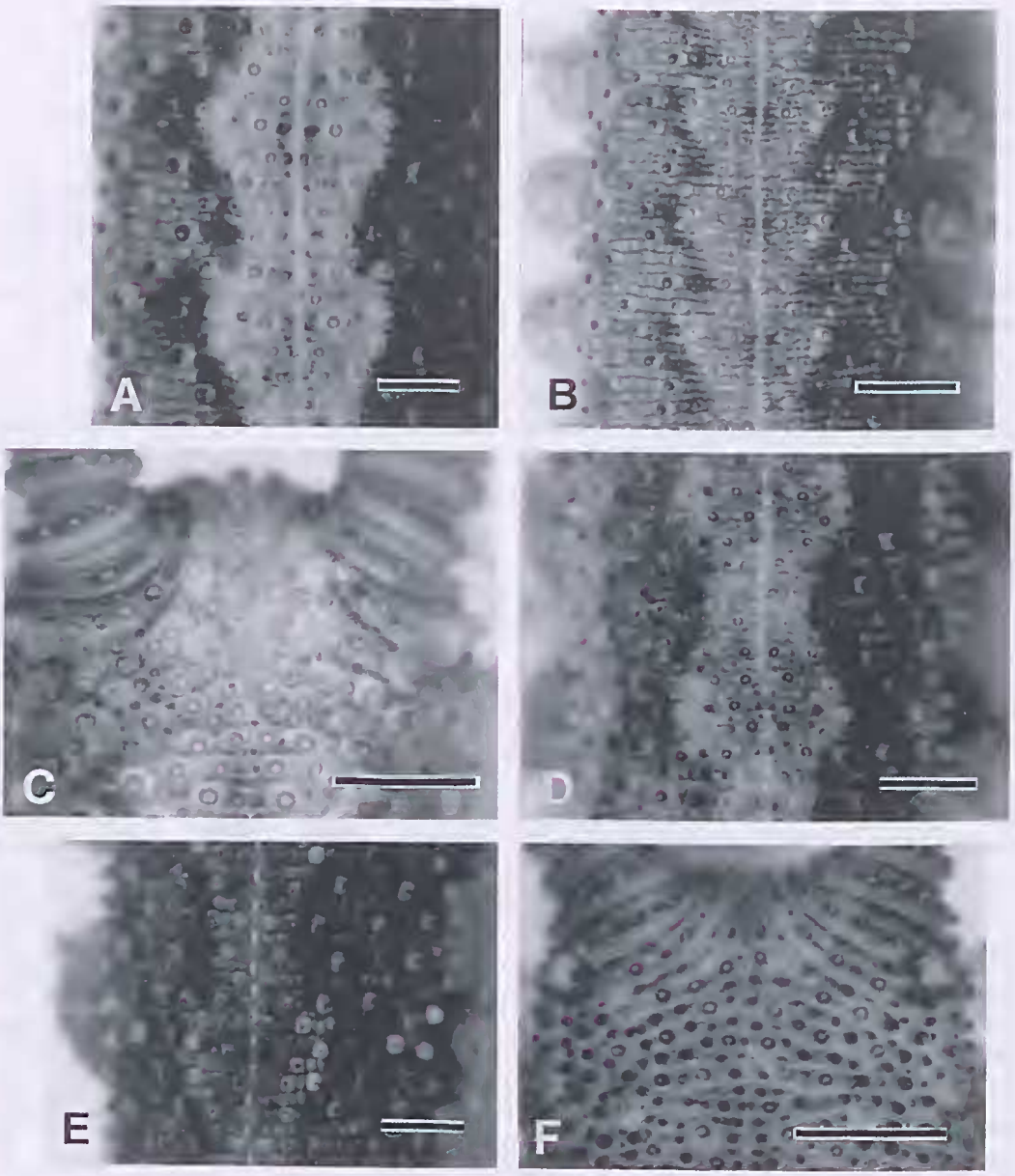


Fig. 6. *Ooperipatus birrgus*, sp. nov.: A, body, dorsal view, holotype male, 1.15 mm HWE, scale bar 0.50 mm. B, body, dorsal view, paratype male, 1.42 mm HWE, scale bar 1 mm. C, head, paratype male, 1.42 mm HWE, scale bar 0.5 mm. *Ooperipatus caesius*, sp. nov.: D, body, dorsal view, paratype female, 1.07 mm HWE, scale bar 0.50 mm. E, body, dorsal view, paratype male, 1.25 mm HWE, scale bar 0.50 mm. F, head, paratype male, 1.25 mm HWE, scale bar 0.50 mm.

rings in adults; antennae with repeating pattern of wide, narrow, wide, very narrow rings; two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 9 and 12; remaining rings with single row of bristles. Distal 8–10 antennal rings with sensory bulbs. Sensory pads with up to four rows of sensilla.

Eyes. EDI males 0.09–0.10–0.11; female 0.11.

Head (males). Males with modified papillae on head (ie. differ from remaining dorsal papillae). Modified papillae positioned mediodorsally, anterior to eyes. Modified papillar scales project outwards from central bristle, appear spiky (Figs 6C; 7A); modified papillae slightly enlarged; all approximately similar sized, distributed evenly from approximately level with eyes to between antennae anteriorly.

Head (females). Females with no modification of head papillae.

Integument. Males with 11, female with 21 papillae counted from mid-dorsal line to junction of oneopod 10. Dorsal body papillae not uniform size; alternate plicae with slightly larger primary papillae; dorsal primary papillae semicircular; papillar scales ribbed in both sexes (Fig. 7B, C); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oneopods in line with junction of oneopods and body.

Oncopods. Sometimes with up to three bristles on anterior and posterior distal foot papillae, median papillae with 1–2 bristles.

Male reproductive tract. Genital pad papillae large (similar size to those on remaining ventral integument), distal papillae not fused. Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from vasa efferentia for a short distance before looping posteriorly toward gonopore.

Male glands and gland papillae. Crural papillae present on ventral side of oneopods 1–14; crural papillae protrude between plicae 4–5 (counting from third spinous pad). Papillae similar in shape on all oneopods: semicircular proximally, tapered abruptly, semicircular or cylindrical distally; with finely ribbed scales basally, distally scales with distinct ribs; smooth region surrounding distal foramen ovoid or lip-shaped, not extending to papillar margin (Fig. 7D–F). Crural glands extend into lateral haemocoel from oneopods 11–13; sometimes folded back along length; remaining glands confined within oneopods. Anterior accessory gland papillae semicircular; foramen a longitudinal slit (Fig. 7G). Anterior accessory glands short; lying in lateral haemocoel, not extending into perivisceral haemocoel; extending anteriorly approximately to oneopods 14; contents opaque white or cream. Posterior accessory gland foramen open approximately midway between genital and anal openings; gland foramen joined medially forming a 'W' shape (Fig. 7H); posterior accessory glands folded distally, long hook tapered only slightly to blunt tip.

Remarks

The female contains well-developed eggs in the oviducts. This species is most similar to *O. hispidus* also from south-eastern NSW. The two species are undoubtedly closely related. They differ in a number of characters. The proximal half of each antennal ring is banded in *O. birrgus*, while every fourth antennal ring is banded in *O. hispidus*. The eyes appear to be larger in *O. birrgus*, than in *O. hispidus* (bearing in mind the small sample size of the former species). Eye diameter indices range from 0.05–0.80 (n = 6) in *O. hispidus* males, and 0.09–0.11 (n = 2) in *O. birrgus males*. Ranges for females are 0.04–0.09 (n = 9) and 0.11 (n = 1), respectively. In *O. hispidus* males, the distal tips of the crural papillae on oneopods 1–10 are pointed, while none are pointed in *O. birrgus*. The crural glands extending into the lateral haemocoel are long and sometimes folded in *O. birrgus*, while they are all relatively short and straight in *O. hispidus*. Differences between *O. birrgus* and other *Ooperipatus* species are shown in Table 2.

Habitat

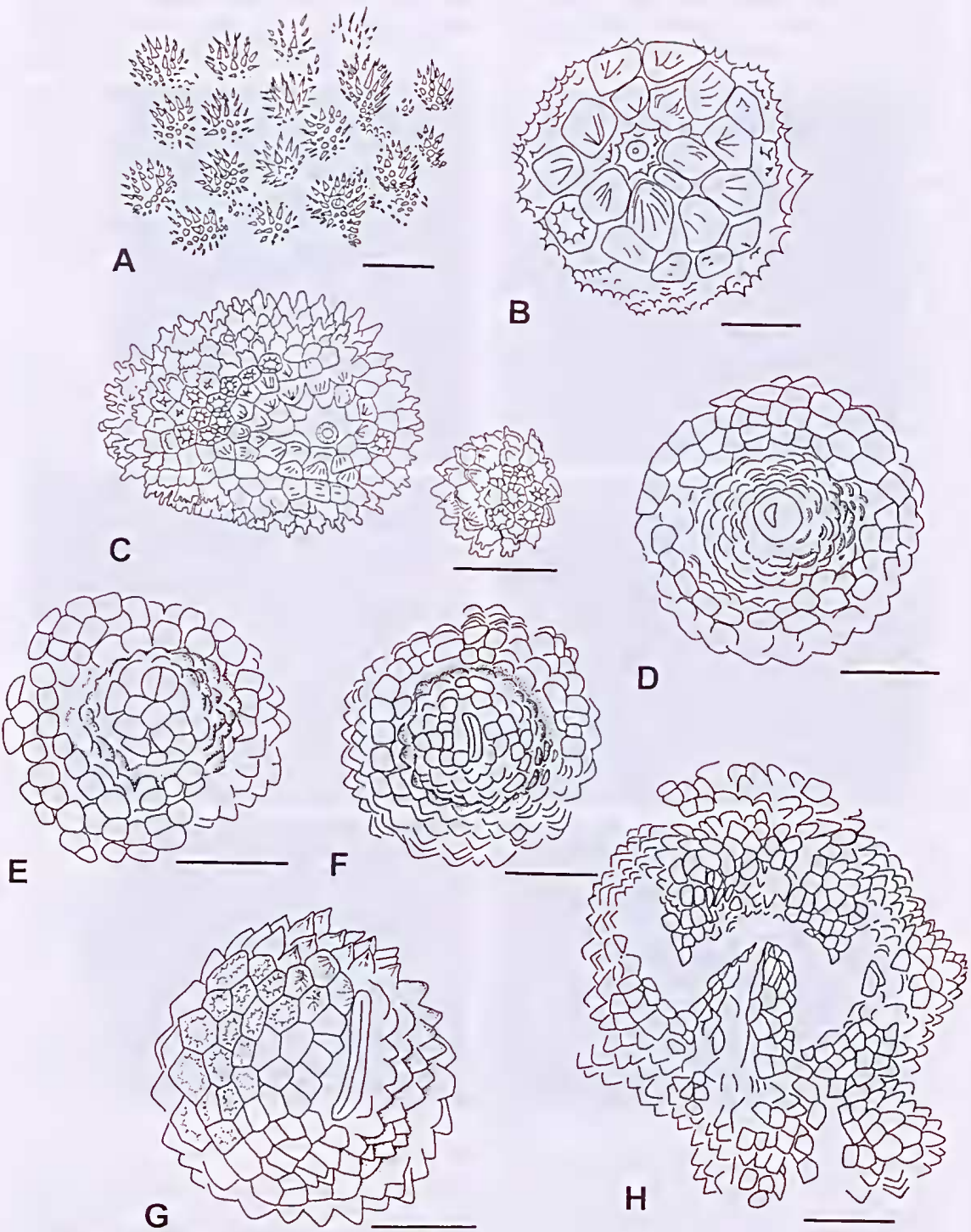
Specimens were found inside a decomposing log. Hand collected specimens were usually lying flat and straight when first exposed.

Distribution

New South Wales, South East Forests NP, 37°01′S, 149°23′E. Known only from the type locality (Figs 5B; 8).

Etymology

The name of this species is derived from the Wiradjuri aboriginal name for scrub, or bush, *birrgun* (McNicol & Hosking 1999) and refers to the habitat in which the species was found.


A
B
C
D
E
F
G
H

Ooperipatus caesius, sp. nov.

Figs 5B; 6D–F; 9A–F; 10

Material examined

Holotype. ♂, Victoria, Mt Buffalo NP, track to Eurobin Falls, 36°43′S,146°50′S, 500 m, 11.iii.1999, coll. A. Reid and R. Roberts (MV K-7318).

Paratypes. Victoria: 6♂, 3♀, data as for holotype (MV K-7319).

Other material examined. Victoria: 1♀, Mt Buffalo NP, Eurobin Falls, 36°43′S,146°50′E, 500 m, 8.iv.1990, coll. D. Black (MV); 1♀, Mt Buffalo NP, near trail entrance to Eurobin Falls, 36°43′S,146°50′E, 8.iv.1990, coll. D. Black (MV).

Diagnosis

Patch of bluish-grey papillae dorsal to each oncopod and tan patches between oncopods. Males with no modification of head papillae. Crural papillae on oncopods 2–3 and 6–14; shape similar on all oncopods, smooth rim surrounding distal foramen ovoid or lip-shaped. Anterior accessory gland foramen an oblique or transverse slit.

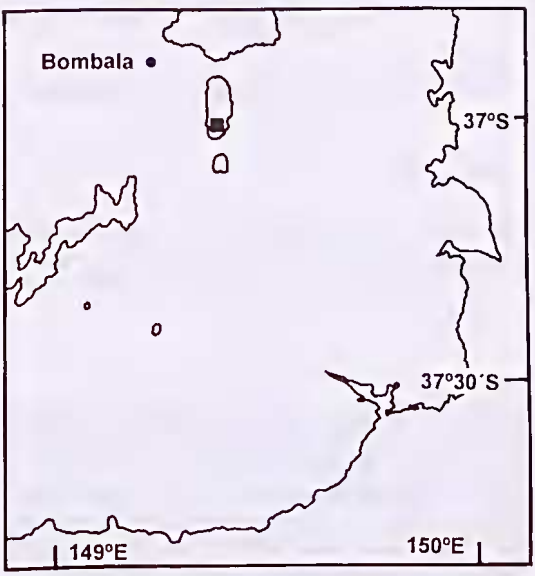


Fig. 8. Ooperipatus birrgus, sp. nov., collection site (solid square). 1000 m contour shown. See Fig. 5B for larger scale map indicating region shown here.

Description

Measurements. HWE males 0.95–1.07–1.25 mm (n = 7, holotype 1.20 mm HWE); females 0.95–1.05–1.12 mm (n = 5).

Color pattern (Fig. 6D, E). Ground-color tan, greyish-blue, olive green, or buff brown; primary papillae light-colored basally, dark tipped. Series of joined diamonds along midline, lateral angles in line with oncopods (can appear scalloped in distended specimens); diamonds lighter-colored than surrounding integument and usually bordered by darker pigment; laterally with light-colored patches between oncopods (tan), and with bluish-grey patches dorsal to oncopods (Fig. 9A). Papillae around anal opening pigmented as for rest of body. Ventral pigment present; with dark patches extending from oncopods to ventral organs. Spinous pads pale yellow, or tan. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally, or not banded, ground-color; dorsal banding on proximal half of each antennal ring (distal half ground-color), with every fourth ring predominantly tan (variable, ventral banding, if present, on every fourth ring only). Greater than 30 antennal rings in adults; antennae with repeating pattern of wide, narrow, wide, very narrow rings; two rows of bristles on rings (counting from distal to proximal) 6, 8, 10 or 11; remaining rings with single row of bristles. Distal 9 antennal rings with sensory bulbs. Sensory pads with up to 3–4 rows of sensilla.

Eyes. EDI males 0.08–0.08–0.10; females 0.07–0.08–0.09.

Head (males). Males with no modification of head

Fig. 7. Ooperipatus birrgus, sp. nov.: A, patch of male modified head papillae, drawn from scanning electron micrograph, scale bar 100 μm. B, primary papilla, paratype male, 1.42 mm HWE, scale bar 0.05 mm. C, primary papilla (left) and secondary papilla (right), paratype female, 1.90 mm HWE, scale bar 0.05 mm. D, crural papilla, oncopod 3, holotype male, 1.15 mm HWE, scale bar 0.05 mm. E, crural papilla oncopod 7, holotype male, 1.15 mm HWE, scale bar 0.05 mm. F, crural papilla oncopod 12, holotype male, 1.15 mm HWE, scale bar 0.05 mm. G, anterior accessory gland papilla, paratype male, 1.42 mm HWE, scale bar 0.05 mm. H, posterior accessory gland foramen, paratype male, 1.42 mm HWE, scale bar 0.05 mm.

Character state	*O. birrgus*, sp. nov.	*O. caesius*, sp. nov.	*O. centunculus* Reid	*O. costatus* Reid	*O. hispidus* Reid
Papillae surrounding anal opening	ground color	ground color	tan	ground color	ground color
Male modified head papillae	spiky	absent	partially fused ridges	fused ridges	spiky
Female modified head papillae	absent	absent	present	present	absent
Male distal papillar scales	ribbed	ribbed	ribs partially fused	ribbed	ribbed
Anterior and posterior distal foot papillae bristles	3	2	1 or 2	2	1 or 2
Oncopods with crural papillae	1–14	2–3 and 6–14	6–14	2–3 and 6–14	1–14
Crural shape	all similar	all similar	all similar	shape differs, some subconical	shape differs, some pointed
Anterior accessory gland papillae foramen	longitudinal	transverse or oblique	U-shaped	longitudinal	curved, short
Anterior accessory glands*	short	long	long	short	short
Posterior accessory gland foramen	joined	separate	separate	separate	joined

Table 2. *Ooperipatus* Dendy, distinguishing character states. *Anterior accessory glands are described as short the level of oncopod 14.

papillae (ie. papillae on head do not differ from remaining dorsal papillae) (Fig. 6F).

Head (females). Females with no modification of head papillae.

Integument. Males with 11–13–18, females with 10–12–14 papillae counted from mid-dorsal line to junction of oncopod 10. Dorsal body papillae not uniform size; alternate plicae with slightly larger primary papillae; dorsal primary papillae semi-circular; papillar scales ribbed in both sexes (Fig. 9B, C); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body.

Oncopods. Two bristles on anterior and posterior distal foot papillae, one bristle on median foot papillae.

Male reproductive tract. Genital pad papillae large, distal papillae not fused. Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens, or separate, do not lie parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from vasa efferentia for a short distance before looping posteriorly toward gonopore.

Male glands and gland papillae. Crural papillae present on ventral side of oncopods 2–3 and 6–14 (papillae reduced on oncopods 14); crural papillae protrude between plicae 7–8 (counting from third spinous pad). Papillae similar in shape on all oncopods: semicircular proximally, tapered abruptly, semicircular or cylindrical distally; with finely ribbed scales basally, distally scales broad, with distinct ribs; smooth region surrounding distal foramen ovoid or lip-shaped, not extending to papillar margin (Fig. 9D). Glands extend into lateral haemocoel from oncopods 11–13; straight,

O. lepidus, sp. nov.	*O. nebulosus*, sp. nov.	*O. oviparus* (Dendy)	*O. porcatus*, sp. nov.	*O. pulchellus* Reid	*O. silvanus*, sp. nov.
ground color	ground color	ground color	ground color	ground color	tan
partially fused, spiky, median depression	slightly spiky	partially fused ridges	partially fused, ridges, spiky, median depression	fused ridges	absent
unknown	absent	present	present	present	absent
ribbed	ribs partially fused	ribs partially fused	ribbed	ribbed	ribbed
2	1 or 2	1 or 2	up to 3	up to 3	2
2–3 and 6–14	1–3 and 6–14	1 or 2–14	2–3 and 6–14	2–3 and 6–14	2–14, or 2–3 and 6–14
shape differs, pointed oncopods 6–8	oncopods 1–3 and 6–10 pointed; 11–14 subconical	all similar	all similar, subconical	all similar	all similar, subconical
longitudinal	long curved	U-shaped	curved, short	curved, short	U-shaped
short	long	long	long	long	long
separate	separate	separate	separate	separate	separate

if they do not extend anteriorly beyond the level of oncopod 14, and long if they extend anteriorly beyond

long, not folded. Anterior accessory gland papillae low, semicircular; foramen a transverse, or oblique slit (Fig. 9E). Anterior accessory glands long; lying freely within perivisceral haemocoel; extending anteriorly approximately to oncopods 11–12; contents opaque white or cream. Posterior accessory gland foramen open approximately midway between genital and anal openings; gland foramen separate (papillae not strongly demarked from surrounding ventral papillae) (Fig. 9F); posterior accessory glands folded distally, long hook tapered only slightly to blunt tip.

Remarks

The lateral color pattern, consisting of a patch of bluish-grey papillae dorsal to each oncopod and tan crescent-shaped patches between these, is distinctive in this species. It is clear in all but one very dark greyish-blue specimen. Like *O. silvanus*, sp. nov. from the Otways, male *O. caesius* do not have modified head papillae. The shape of the anterior accessory gland papillar foramen differs: it is U-shaped in *O. silvanus*, sp. nov. and straight in *O. caesius*. The papillae surrounding the anal opening are pigmented as for the rest of the body in *O. caesius* and tan in *O. silvanus*, sp. nov. Differences between *O. caesius* and other *Ooperipatus* species are shown in Table 2.

Habitat

In and under rotting logs and among sieved wood and eucalypt litter. Hand collected specimens were usually lying flat and straight when first exposed.

Distribution

Victoria, Mt Buffalo NP, Eurobin Falls, 36°43′S, 146°50′E (Figs 5B; 10). Known only from the

type locality.

Etymology

The Latin speeific name means 'bluish-grey' and refers to the color of the patch of papillae above the oncopods in this speeies.

Ooperipatus lepidus, sp. nov.

Figs 5B; 10; 11A, B; 12A–F

Material examined

Holotype. ♂, Victoria, Granite Flat, 9 km S of Mitta Mitta, beside Omeo Hwy, 350 m N of intersection of Omeo Hwy and Walsh's Rd, 36°35'S,147°27'E, 340 m, 9.iii.1999, coll. A. Reid and R. Roberts (MV K-7320). *Paratype*. Victoria: 1♂, data as for holotype (MV K-7321).

Diagnosis

Males with triangular patch of modified papillae on head; modified papillae in middle of patch partially fused, redueed, spiky; papillae on each side of this region almost eompletely fused forming spiky ridges. Crural papillae on oneopods 2–3 and 6–14; papillae on oneopods 2–3 and 9–14 eylindrical distally; papillae on oneopods 6–8 eonical, pointed distally. Anterior aeeessory glands short, extending anteriorly to oncopods 14.

Description

Measurements. HWE males 1.25–1.31–1.37 mm (n = 2, holotype 1.37 mm HWE).
Color pattern (Fig. 11A). Ground-color olive green,

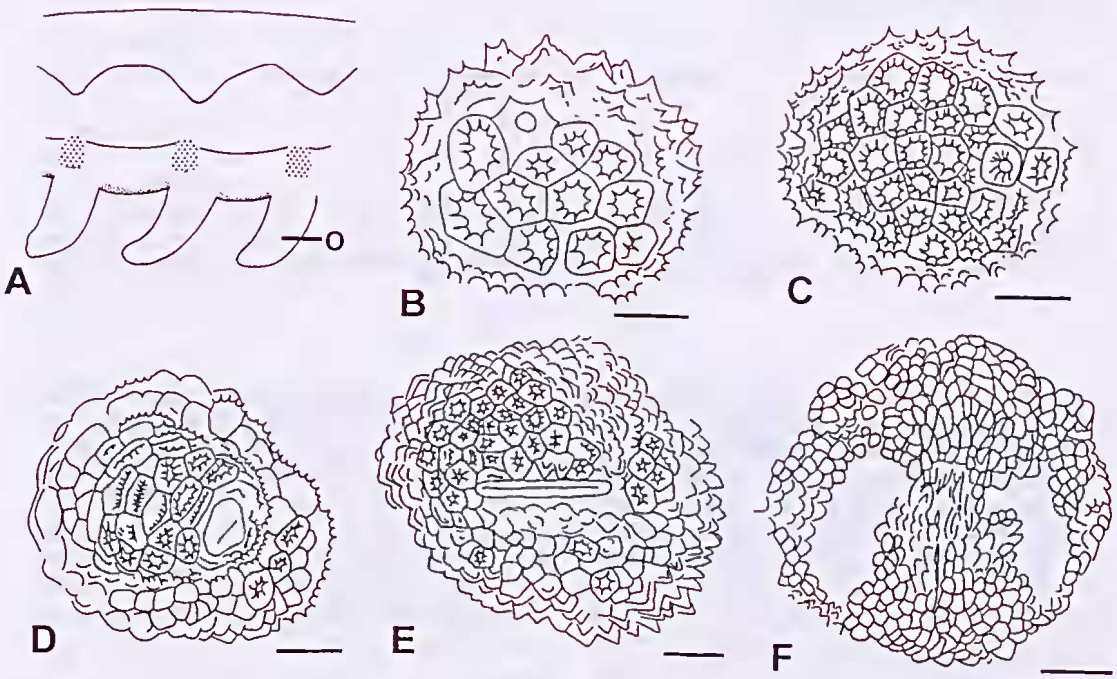


Fig. 9. Ooperipatus caesius, sp. nov.: A, diagram to show characteristic lateral patterning, shaded spots correspond to bluish-grey patches dorsal to oncopods (O). B, primary papilla, paratype male 0.97 mm HWE, scale bar 0.02 mm. C, primary papilla, paratype female 1.07 mm HWE, scale bar 0.02 mm. D, crural papilla oncopod 7, paratype male, 0.97 mm HWE, scale bar 0.02 mm. E, anterior accessory gland papilla, paratype male, 0.97 mm HWE, scale bar 0.02 mm. F, posterior accessory gland foramen, paratype male, 0.97 mm HWE, scale bar 0.05 mm.

or brown; primary papillae light-colored basally, dark tipped. Series of joined diamonds along midline, lateral angles in line with oncopods (can appear scalloped in distended specimens); diamonds lighter-colored than surrounding integument and usually bordered by darker pigment; laterally with longitudinal light-colored band dorsal to oncopods (not pronounced). Papillae around anal opening pigmented as for rest of body. Ventral pigment present; dark patches between ventral organs and oncopods. Spinous pads pale yellow, or tan. Integument between genital and anal openings pigmented as for rest of ventrum.

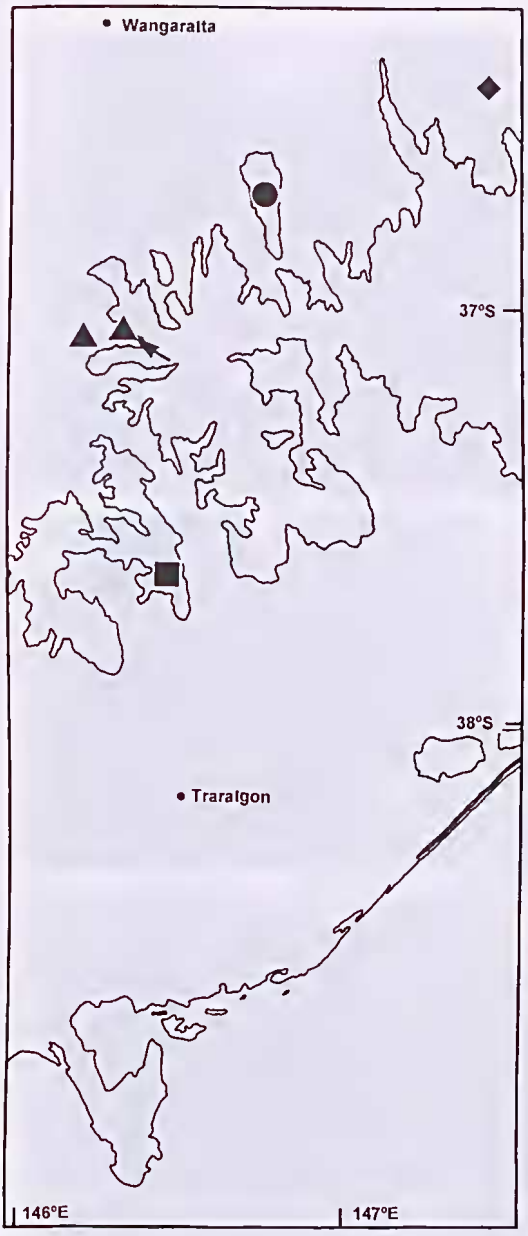


Fig. 10. Collection sites: *Ooperipatus caesius*, sp. nov. (large circle); *O. lepidus*, sp. nov. (diamond); *O. nebulosus*, sp. nov. (triangles), arrow indicates type locality; *O. porcatus*, sp. nov. (square). 1000 m contour shown. See Fig. 5B for larger scale map indicating region shown here.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally; dorsal banding on every eighth ring (or every sixth if very narrow rings not counted), or on proximal half of each antennal ring (distal half ground-color). Greater than 30 antennal rings in adults; antennae with repeating pattern of wide, narrow, wide, very narrow rings; two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 9 and 12; remaining rings with single row of bristles. Distal 11 antennal rings with sensory bulbs. Sensory pads with up to six rows of sensilla.

Eyes. EDI males 0.09–0.10–0.11.

Head (males). Males with modified papillae on head (ie. differ from remaining dorsal papillae). Modified papillae positioned mediodorsally anterior to eyes, forming triangular patch (Figs 11B; 12A). Modified papillae extending anteriorly from level of eyes; modified papillae in middle of patch partially fused, spiky, reduced, forming a shallow, triangular depression; papillae on each side of this region almost completely fused forming ridges, spiky (Fig. 12A).

Integument. Males with 13–14–15 papillae counted from mid-dorsal line to junction of oncopod 10. Dorsal body papillae not uniform size; alternate plicae with markedly larger primary papillae; dorsal primary papillae semicircular; papillar scales ribbed in males (Fig. 12B); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body.

Oncopods. Two bristles on anterior and posterior distal foot papillae, one bristle on median foot papillae.

Male reproductive tract. Genital pad papillae large, distal papillae not fused; tan in both specimens. Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly

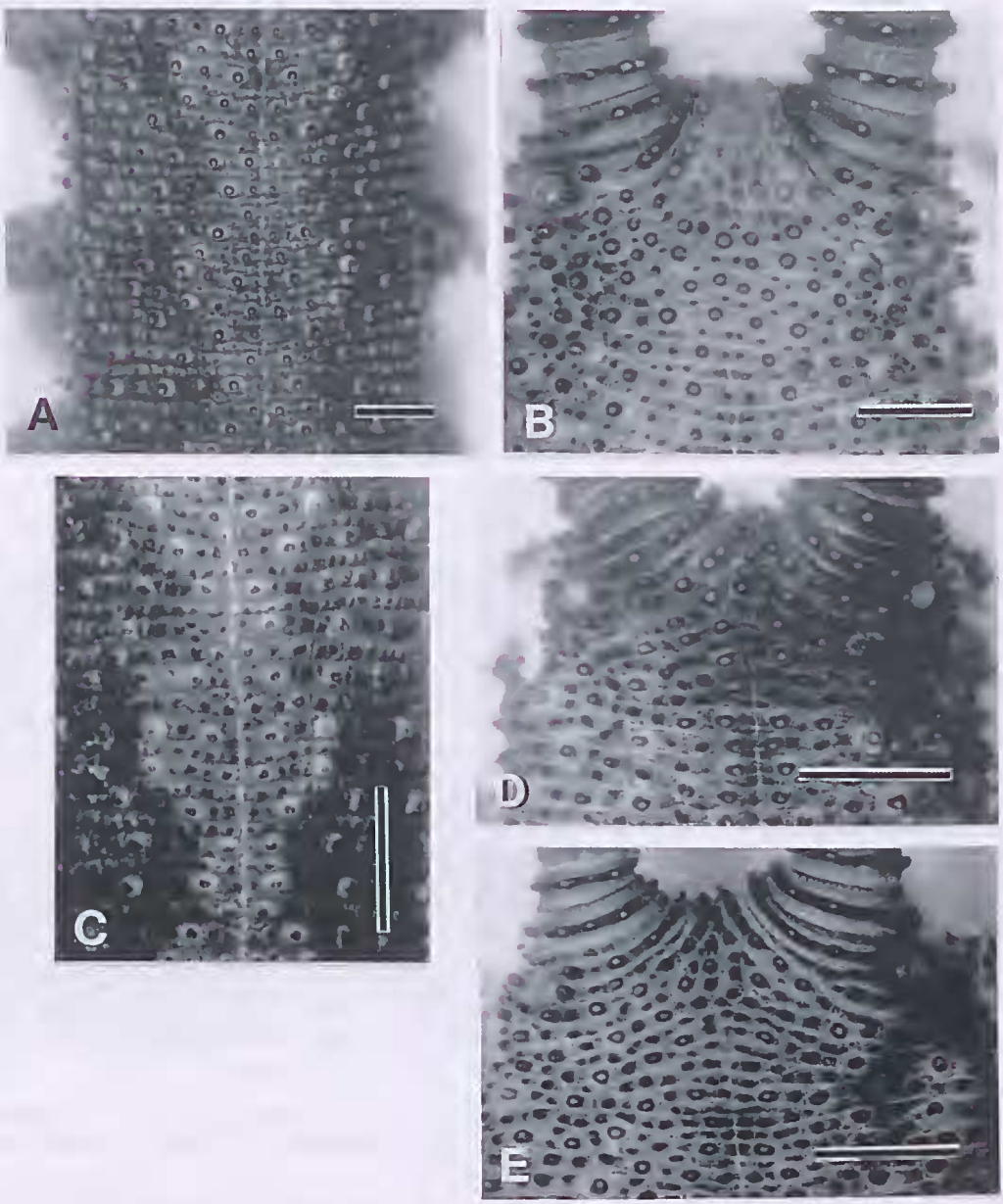


Fig. 11. *Ooperipatus lepidus*, sp. nov.: A, body, dorsal view, holotype male, 1.37 mm HWE, scale bar 0.50 mm. B, head, holotype male, 1.30 mm HWE, scale bar 0.50 mm. *Ooperipatus nebulosus*, sp. nov.: C, body, dorsal view, paratype female 1.30 mm HWE, scale bar 1 mm. D, head, holotype male 1.17 mm HWE, scale bar 0.05 mm. E, head, paratype female 1.25 mm HWE, scale bar 0.5 mm.

from paired vasa efferentia for short distance before looping posteriorly toward gonopore.

Male glands and gland papillae. Crural papillae present on ventral side of oncopods 2–3 and 6–14 (see *Remarks*); crural papillae protrude between plicae 4–5 (counting from third spinous pad). Papillar shape differs among oncopods: semicircular proximally, tapered abruptly, semicircular or cylindrical distally on oncopods 2–3 and 9–14 (Fig. 12C, F) or broad based, semicircular proximally, tapered abruptly, conical distally on oncopods 6–8 (Fig. 12D, E); with finely ribbed scales basally, distally scales with distinct ribs; smooth region surrounding distal foramen ovoid or lip-shaped, not extending to papillar margin (Fig. 12F), or narrow, pointed, subconical (Fig. 12D, E). Glands extend into lateral haemocoel from oncopods 11–13; sometimes folded back along length; remaining glands confined within oncopods. Anterior accessory gland papillae low, semicircular; foramen a longitudinal slit. Anterior accessory glands short; lying freely within perivisceral haemocoel, or lying in lateral haemocoel, not extending into perivisceral haemocoel; extending anteriorly approximately to oncopods 14; contents opaque white or cream. Posterior accessory gland foramen open approximately midway between genital and anal openings; gland foramen separate, close together; posterior accessory glands folded distally, long hook tapered only slightly to blunt tip.

Remarks

While the females are unknown, the males clearly conform to *Ooperipatus* and have a significant number of distinctive features that justify the description of *O. lepidus* at this time. Crural papillae are not visible on oncopods 2 and 3 in the holotype and are reduced on oncopods 2 of the paratype. They are retracted in both specimens. The arrangement of modified head papillae in males is similar to *O. porcatus*, sp. nov., but the two species differ in a number of other characters. The antennal sensory pads have up to six rows of sensilla in *O. lepidus*, while there are only 3–4 rows in *O. porcatus*, sp. nov. The distal tips of the crural papillae are all subconical in *O. porcatus*, sp. nov., but are pointed on oncopods 6–8 in *O. lepidus*. The shape of the anterior accessory foramen is a longitudinal slit and anterior accessory glands short in *O. lepidus*, while the gland foramen is a curved, short slit and the anterior accessory glands long in *O. porcatus*, sp. nov. The *O. lepidus* specimens were found under logs with *Planipapillus berti* Reid (2000). Differences between *O. lepidus* and other *Ooperipatus* are shown in Table 2.

Habitat

Specimens were found under decomposing logs. Hand collected specimens were lying flat and straight when first exposed.

Distribution

Victoria, Granite Flat, 36°35′S,147°27′E (Figs 5B; 10). Known only from the type locality.

Etymology

The Latin specific name means 'fine' or 'elegant'.

Ooperipatus nebulosus, sp. nov.

Figs 5B; 10; 11C–E; 13A–G

Material examined

Holotype. ♂, Victoria, 11 km E of Merrijig, Carters Hill Reserve, 950 m along Carters Rd from Mt Buller Rd, 37°06′S,146°22′E, 640 m, 20.xi.1999, coll. A. Reid and R. Roberts (MV K-7322).

Paratypes. Victoria: 4♂, 7♀, 2 juv., data as for holotype (MV K-7323).

Other material examined. Victoria: 2♀, Merrijig, 4.vi. 1998, coll. N. N. Tait and D. A. Briscoe (MV).

Diagnosis

Male head papillae only slightly spiky, not fused. Remaining papillar scales ribbed proximally, not ribbed distally in males; ribbed in females. Crural papillae on oncopods 1–3 and 6–14; papillae on oncopods 1–3 and 6–10 conical, pointed distally, rest blunt. Anterior accessory gland foramen a long, slightly curved slit. Anterior accessory glands long.

Measurements. HWE males 0.95–1.09–1.20 mm (n = 5, holotype 0.75 mm HWE); females 0.92–1.28–1.45 mm (n = 7).

Color pattern (Fig. 11C). Ground-color grey, olive green, or buff brown (dark); primary papillae light-colored basally, dark tipped. Series of joined diamonds along midline, lateral angles in line with oncopods (can appear scalloped in distended specimens); diamonds lighter-colored than

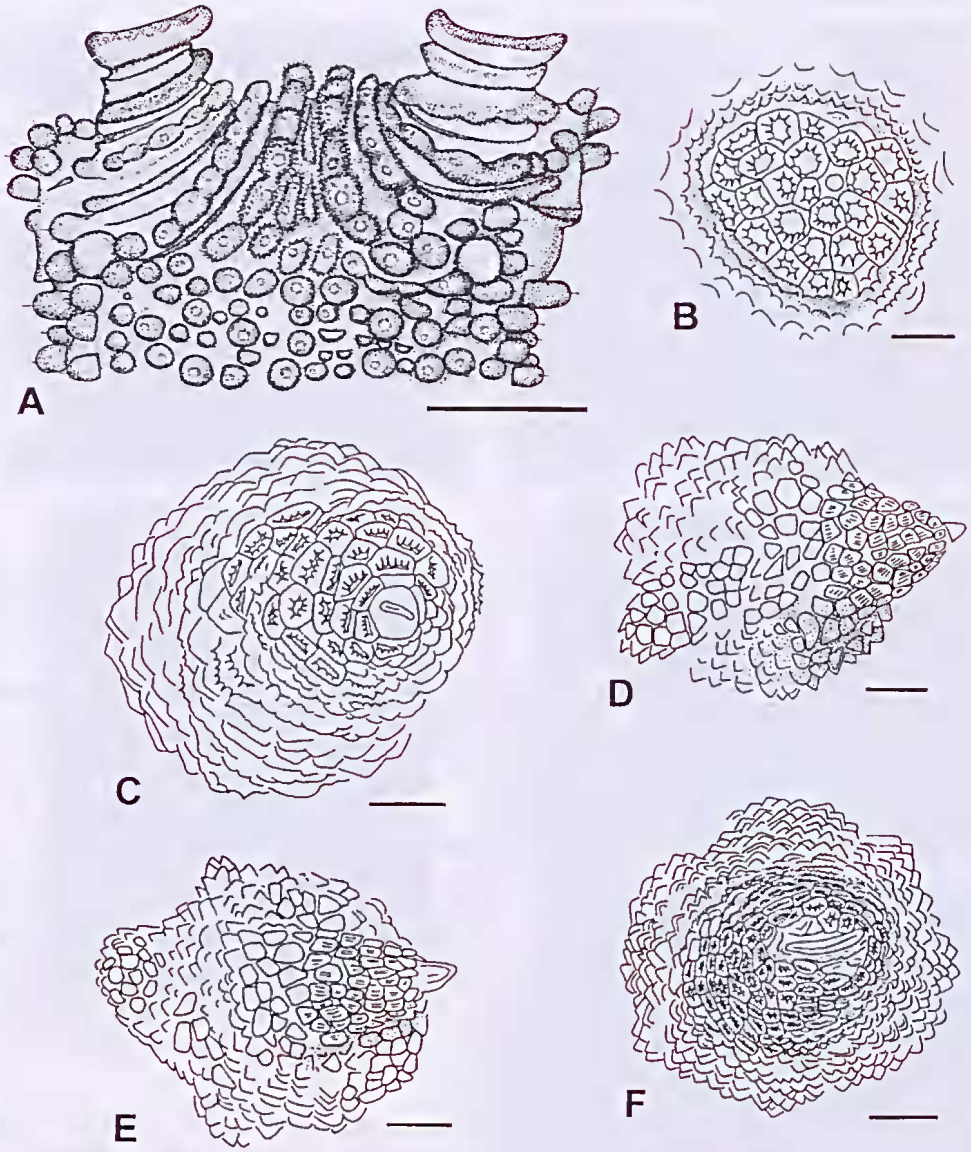


Fig. 12. *Ooperipatus lepidus*, sp. nov.: A, head, paratype male, 1.25 mm HWE, scale bar 0.50 mm. B, primary papilla, paratype male 1.25 mm HWE, scale bar 0.02 mm. C, crural papilla, oncopod 3, paratype male 1.25 mm HWE, scale bar 0.02 mm HWE. D, crural papilla, oncopod 7, holotype male 1.37 mm HWE, scale bar 0.03 mm. E, crural papilla oncopod 8, holotype male 1.37 mm HWE, scale bar 0.03 mm. F, crural papilla, oncopod 12, paratype male 1.25 mm HWE, scale bar 0.04 mm.

surrounding integument and usually bordered by darker pigment; laterally with longitudinal light-colored band dorsal to oncopods, or with light-colored patches between oncopods. Papillae around anal opening pigmented as for rest of body. Ventral pigment present; usually with dark patches extending from oncopods to ventral organs. Spinous pads pale yellow, or greyish-blue. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally (only sometimes ventrally), or not banded, ground-color; dorsal banding on every fourth ring distal to and including ring five, or sometimes a trace of banding on proximal half of each antennal ring (distal half ground-color). Approximately 30 antennal rings in adults and juveniles; antennae with repeating pattern of wide, narrow, wide, very narrow rings; single row of bristles on each antennal ring, or two rows of bristles on rings (counting from distal to proximal) 3, 4, 6, 8 and 11; remaining rings with single row of bristles. Distal 9–10 antennal rings with sensory bulbs. Sensory pads with up to three rows of sensilla.

Eyes. EDI males 0.06–0.07–0.08; females 0.05–0.07–0.09.

Head (males). Males with modified papillae on head (ie. differ from remaining dorsal papillae). Modified papillae positioned mediodorsally, anterior to eyes, concentrated medially. Modified papillar scales project outwards from central bristle, appear spiky (but not pronounced) (Fig. 11D).

Head (females). Females with no modification of head papillae (Fig. 11E).

Integument. Males with 10–12–13 papillae counted from mid-dorsal line to junction of oncopod 10, females with 10–16–24 papillae counted from mid-dorsal line to junction of oncopod 10. Dorsal body papillae not uniform size; alternate plicae with slightly larger primary papillae; dorsal primary papillae semicircular; papillar scales ribbed proximally (microcristae well defined), not ribbed distally (microcristae fused) in males (Fig. 13A); ribbed in females (Fig. 13B); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oncopods in line with junction of oncopods and body; papillae around anal opening slightly larger than those on rest of body (Fig. 13C).

Oncopods. Distal foot papillae each with single sensory bristle (usually), or two bristles on anterior and posterior distal foot papillae, one bristle on median foot papillae.

Male reproductive tract. Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from vasa efferentia for a short distance before looping posteriorly toward gonopore.

Male glands and gland papillae. Crural papillae present on ventral side of oncopods 1–3 and 6–14; crural papillae protrude between plicae 5–6 (counting from third spinous pad). Papillar shape differs among oncopods: broad based, semicircular proximally, tapered abruptly, conical distally on oncopods 1–3 and 6–10 (Fig. 13D, E) or semicircular proximally, tapered abruptly, semicircular or cylindrical distally on oncopods 11–14 (Fig. 13F); with finely ribbed scales basally, distally scales with distinct ribs; smooth region surrounding distal foramen narrow, pointed, subconical oncopods 1–3 and 6–10 (Fig. 13D, E), or ovoid or lip-shaped, not extending to papillar margin on oncopods 11–14 (Fig. 13F). Glands extend into lateral haemocoel from oncopods 11–14; straight, short, not folded; remaining glands confined within oncopods. Anterior accessory papillae broad, semicircular; foramen a curved longitudinal slit (Fig. 13C). Anterior accessory glands long; lying freely within perivisceral haemocoel; extending anteriorly approximately to oncopods 11–12; contents opaque white or cream. Posterior accessory glands open approximately midway between genital and anal openings; gland foramen separate, close together (Fig. 13C); posterior accessory glands folded distally, short blunt hook (Fig. 13G).

Remarks

The *O. nebulosus* male head papillae are only slightly spiky, but otherwise do not differ significantly from the remaining head papillae. *Ooperipatus caesius* and *O. silvanus*, sp. nov., males do not have modified head papillae. *Ooperipatus nebulosus* differs from both these species in having pointed, rather than blunt crural papillae on some of the oncopods, and distal papillar scales with partially fused ribs in males. In addition, *O. nebulosus* has crural papillae on the first pair of oncopods, unlike *O. caesius* and *O. silvanus*, sp. nov. The anterior accessory gland foramen is a distinct U-shape in *O. silvanus*, sp. nov., but only slightly curved in *O. nebulosus*. Differences between *O. nebulous* and other

Ooperipatus are shown in Table 2.

Some of the large females contained well-developed eggs in the oviducts.

Habitat

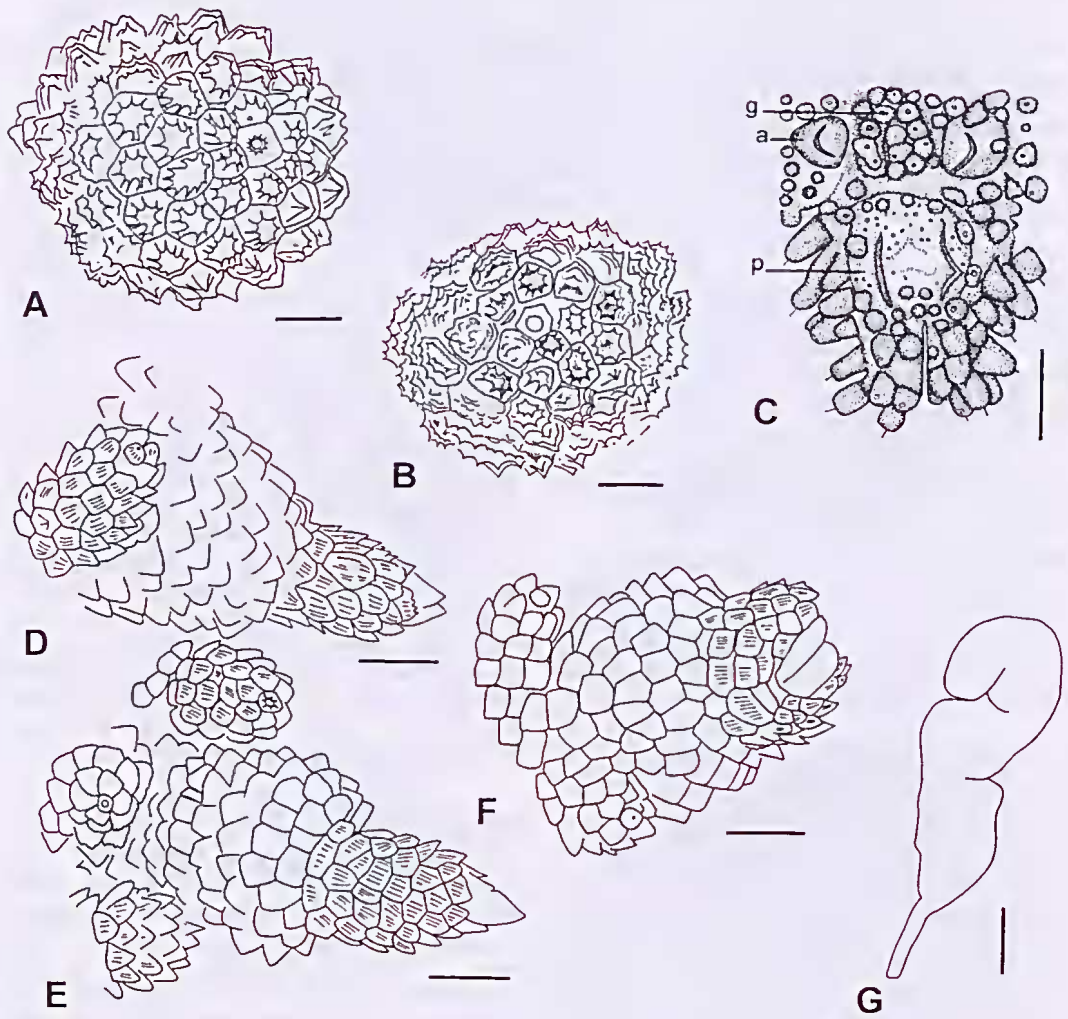


Fig. 13. Ooperipatus nebulosus, sp. nov.: A, primary papilla, paratype male, 1.20 mm HWE, scale bar 0.02 mm. B, primary papilla, paratype female, 1.25 mm HWE, female, scale bar 0.02 mm. C, ventro-posterior end of paratype male, 1.20 mm HWE, scale bar 0.30 mm (a, anterior accessory gland papillae; g, genital pad; p, posterior accessory gland foramen). D, crural papilla, oncopod 3, holotype male, 1.17 mm HWE, scale bar 0.04 mm. E, crural papilla, oncopod 7, holotype male, 1.17 mm HWE, scale bar 0.04 mm. F, crural papilla, oncopod 12, holotype male, 1.17 mm HWE, scale bar 0.04 mm. G, posterior accessory gland, paratype male 1.20 mm HWE, scale bar 0.02 mm.

Under logs in dry selerophyll forest.

Distribution

Victoria, Merrijig to 11 km E of Merrijig, Carters Hill Reserve, 37°06′S,146°15′E–37°06′S,146°22′E (Figs 5B; 10).

Etymology

The Latin speeifie name, *nebulosus*, means 'misty', 'cloudy' or 'dark', and refers to the dark grey color of this species.

Ooperipatus poreatus, sp. nov.

Figs 5B; 10; 14A–C; 15A–G

Material examined

Holotype. ♂, Victoria, Mt Useful Scenic Reserve, 14.5 km N of intersection of Binns Rd and McEvoys Tk, 37°43′S,146°31′E, 750 m, 3.iv.1999, coll. A. Reid and R. Roberts (MV K-7324).

Paratypes. Victoria: 3♂, 8♀, data as for holotype (MV K-7325).

Diagnosis

Males with triangular patch of modified papillae on head; modified papillae reduced, partially fused, some spiky. Crural papillae on oneopods 2–3 and 6–14, all broad basally, subconical distally; smooth region surrounding crural papillae foramen extending around rim to envelop distal margin. Anterior aeeessory glands long, extending anteriorly to oneopod 13.

Measurements. HWE males 1.12–1.25–1.32 mm (n = 4, holotype 1.30 mm HWE); females 1.12–1.36–1.5 mm (n = 8).

Color pattern (Fig. 14A, B). Ground-color grey, olive green, or brown; primary papillae light-colored basally, dark tipped. Series of joined diamonds along midline, lateral angles in line with oncopods (ean appear scalloped in distended specimens); diamonds lighter-colored than surrounding integument and usually bordered by darker pigment; prominent tan or eream papilla on outer margin of lateral angle of diamonds; tan or eream papillae coneentrated toward lateral angle in short ereseent (Fig. 14B); laterally with longitudinal light-colored band dorsal to oneopods, or without pattern, color as for rest of body. Papillae around anal opening pigmented as for rest of body. Ventral pigment present; with dark patches extending from oncopods to corresponding ventral organs. Spinous pads pale yellow, tan, or greyish-blue. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan or with tan mottle dorsally and ventrally (sometimes trace only; not all speeimens with ventral banding); dorsal banding on every eighth ring (or every sixth if very narrow rings not counted). Greater than 30 antennal rings in adults; antennae with repeating pattern of wide, narrow, wide, very narrow rings; two rows of bristles on rings (counting from distal to proximal) 3, 4, 5, 7, 9 and rarely 12 and 15 (sometimes single row on rings 5 and 7; arrangement differs in small specimens); remaining rings with single row of bristles. Distal 9–10 antennal rings with sensory bulbs. Pads with up to 3–4 rows of sensilla.

Eyes. EDI males 0.07–0.08–0.09; females 0.06–0.08–0.10.

Head (males). Males with modified papillae on head (ie. differ from remaining dorsal papillae). Modified papillae positioned mediodorsally, extending anteriorly from level of eyes, forming triangular patch; three median rows of papillae partially fused, reduced, ridge-like, forming a shallow, triangular depression (Figs 14C; 15A); papillae on either side of this region slightly enlarged, spiky.

Head (females). Females with modified head papillae. Papillae fused or partially fused forming ridges; ridges not as prominent as those seen in males (in larger females only).

Integument. Males with 12–14–15 papillae, females with 10–14–17 papillae counted from mid-dorsal line to junetion of oneopod 10. Dorsal body papillae not uniform size; alternate plieae with slightly larger primary papillae; dorsal primary papillae semieireular; papillar scales ribbed in both sexes (Fig. 15B); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oneopods in line with junction of oncopods and body.

Oncopods. Sometimes with up to three bristles on anterior and posterior distal foot papillae, one bristle on median foot papillae.

Male reproductive tract. Genital pad papillae large,

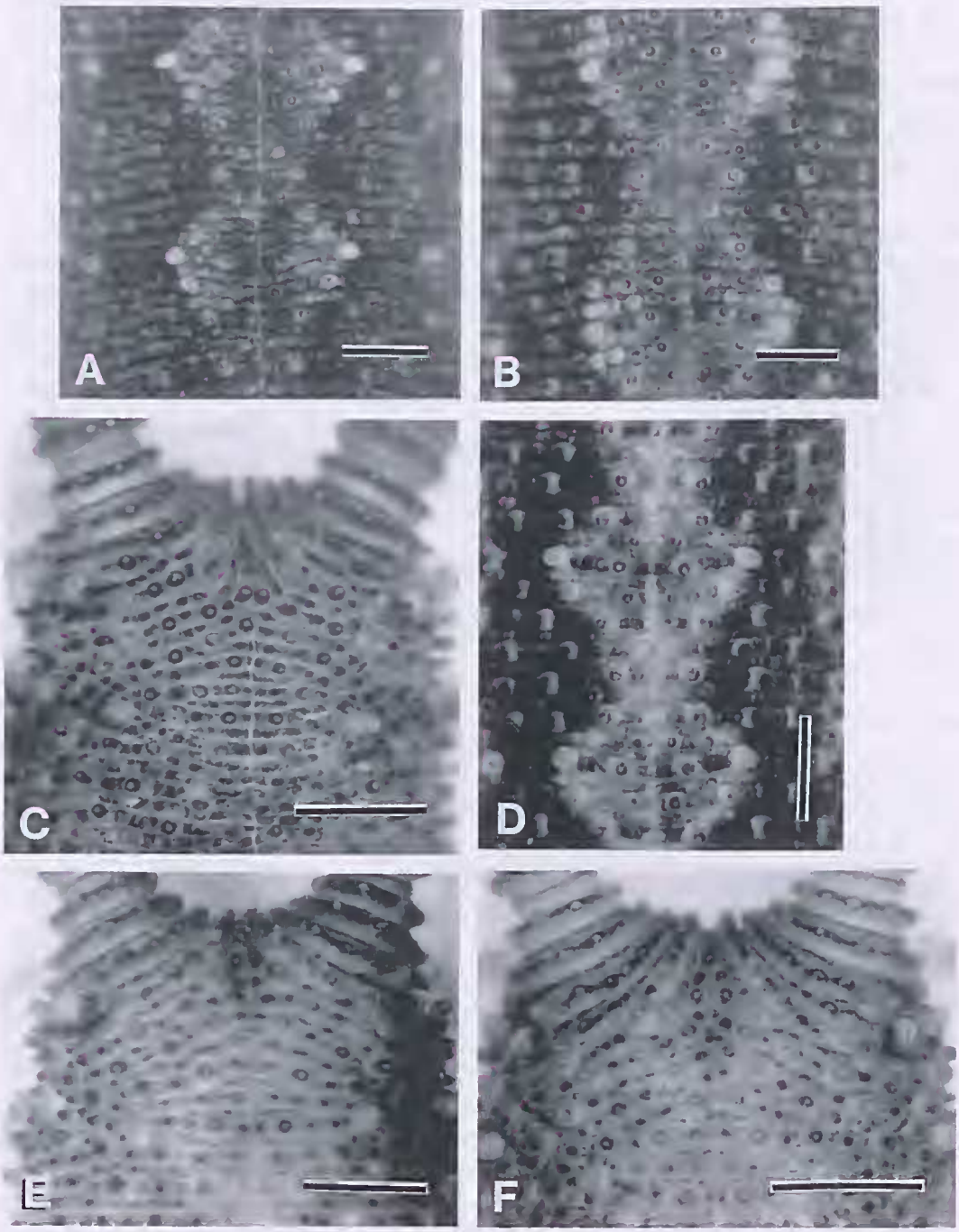


Fig. 14. *Ooperipatus porcatus*, sp. nov.: A, body, dorsal view, holotype male, 1.30 mm HWE, scale bar 0.50 mm. B, body, dorsal view, paratype female, 1.50 mm HWE, scale bar 0.50 mm. C, head, holotype male, 1.30 mm HWE, scale bar 0.50 mm. *Ooperipatus silvanus*, sp. nov.: D, body, dorsal view, paratype male, 1.25 mm HWE, scale bar 0.50 mm. E, head, paratype male, 1.40 mm HWE, scale bar 0.50 mm. F, head, paratype female, 1.25 mm HWE, scale bar 0.50 mm.

some distal papillae fused. Proximal vasa efferentia lying close together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from paired vasa efferentia for short distance before looping posteriorly toward gonopore (Fig. 15C).

Male glands and gland papillae. Crural glands present on ventral side of oncopods 2–3 and 6–14 (greatly reduced on oncopod 14); crural papillae protrude between plicae 4–5 (counting from third spinous pad). Papillae similar in shape on all oncopods: broad based, semicircular, proximally, tapered abruptly, subconical distally; with finely ribbed scales basally, distally scales with distinct ribs; smooth region surrounding distal foramen extending around rim to envelop distal margin (Fig. 14D–G). Crural glands extend into lateral haemocoel from oncopods 6–13; sometimes folded back along length; remaining glands confined within oncopods. Anterior accessory gland papillae low, semicircular, smaller than posterior crural papillae; foramen a slightly curved, short slit. Anterior accessory glands long (Fig. 15C); lying freely within perivisceral haemocoel; extending anteriorly approximately to oncopods 13; contents opaque white or cream. Posterior accessory gland foramen open approximately midway between genital and anal openings; gland foramen separate, close together; posterior accessory glands folded distally, long hook tapered only slightly to blunt tip (Fig. 15C).

Remarks

The gonopore of one female specimen was swollen distally with two openings. All other females had normal gonopores with a single opening, so it seems that the former is an anomalous specimen. *Ooperipatus hispidus, O. lepidus* and *O. nebulosus* all have some crural papillae that are smooth distally around the opening. In *O. porcatus*, all crural papillae are modified, while in the former three species, only some crural papillae are smooth distally. The head papillae of male *O. hispidus* are all spiky: unlike those of *O. porcatus*. *Ooperipatus nebulosus* has crural papillae on the first oncopod pair, and papillar scales that ribbed proximally, but not distally on the rest of the body: unlike *O. porcatus*. The male head papillae also differ in these two species. Differences between *O. lepidus* and *O. porcatus* are given in the *Remarks* section of the *O. lepidus* description. Other differences between these three species and *O. porcatus*, and differences between *O. porcatus* and other *Ooperipatus* are shown in Table 2.

Habitat

In and under rotting logs. Hand collected specimens were usually lying flat and straight when first exposed.

Distribution

Victoria, Mt Useful Scenic Reserve, 37°43′S, 146°31′E (Figs 5B; 10). Known only from the type locality.

Etymology

The Latin specific name, *porcatus*, means 'ridge between two furrows', and refers to the modified head papillae in this species.

Ooperipatus silvanus, sp. nov.

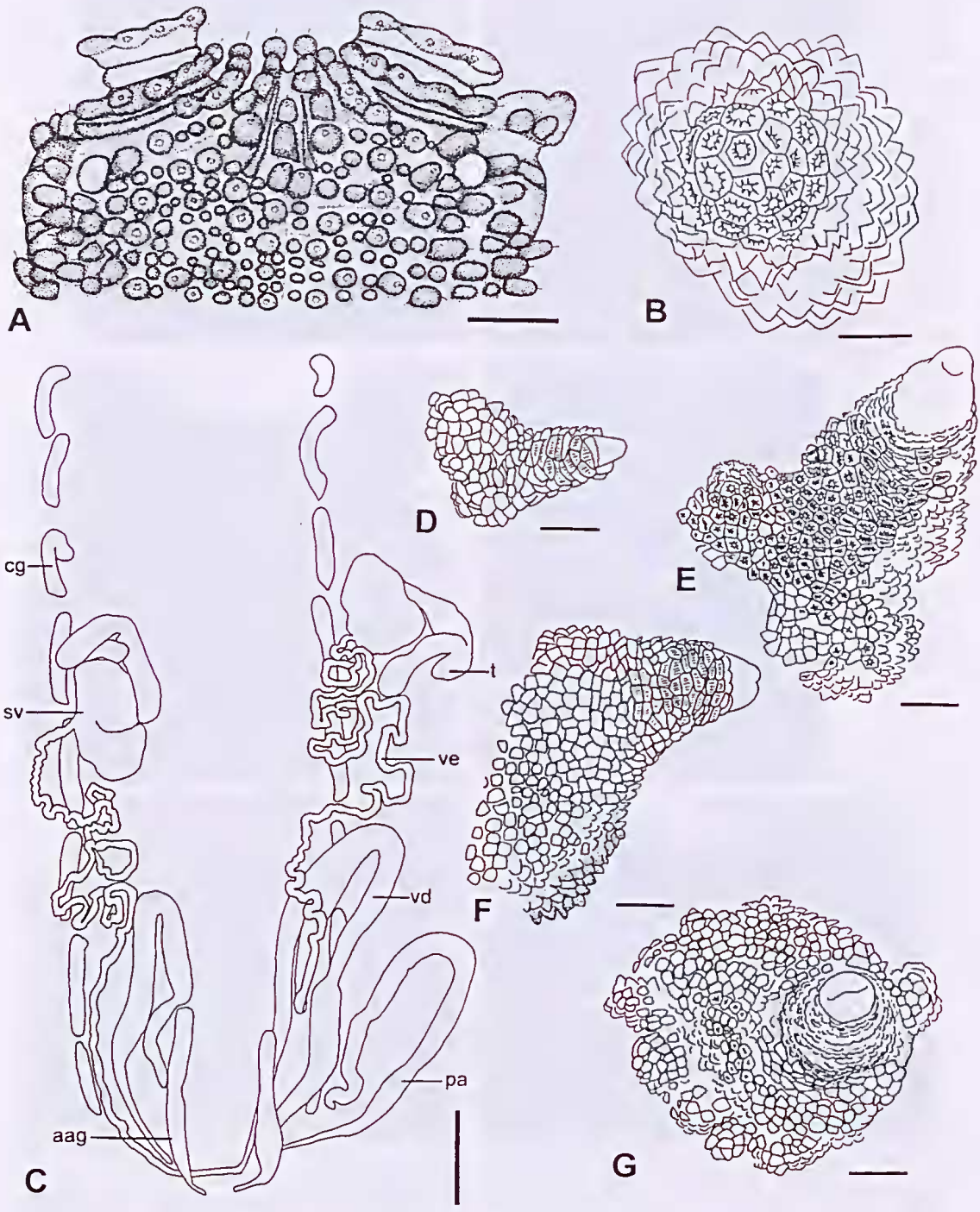
Figs 5B; 14D–F; 16A–E; 17

Material examined

Holotype. ♂, Victoria, Otway Range, 0.1 km S of intersection of Young Ck Tk and Philips Rd, 38°40′S, 143°30′E, 260 m, 19.v.1999, coll. A. Reid and A. Skates (MV K-7326).

Paratypes. Victoria: 1♂, 1♀, data as for holotype (MV K-7327); 3♂, 1♀, Otway Range, 6.5 km S of Gellibrand, 38°34′S,143°31′E, 220 m, 18.v.1999, coll. A. Reid and A. Skates (MV K-7328); 1♂, 1♀, Otway Range, 0.8 km S of intersection of Henrys Rd and Sunnyside Rd, 550 m, 17.v.1999, coll. A. Reid and A. Skates (MV K-7329); 1♀, Otway Range, Aire Ck crossing, 38°42′S, 143°28′E, 220 m, 20.v.1999, coll. A. Reid and A. Skates (MV K-7330).

Other material examined. Victoria: 1♂, Gelibrand, 38°31′S,143°32′E, 19–23.i.1932, coll. J. Clark (MV); 1♀, Forrest, Fossett's property, 38°31′S,143°43′E, 19.xii.1946 (MV); 1 juv., Otway Range, 6.5 km S of Gellibrand, 38°34′S,143°31′E, 220 m, 24.ii.1991, coll. D. Black (MV); 1♂, Otway Range, Mt Sabine 38°38′S,143°44′E, 585 m, 8.iii.1986, coll. M. S. Harvey and B. J. Scott (MV); 2♀, Beech Forest, 38°38′S,143°34′E, 11–19.i.1932, coll. J. Clark (MV); 1♀, Chapple Ck, 20.x.1970 (MV); 1♂, Otway Range, 3.5 km N of Kawarren, 38°39′S,143°34′E, 24.ii.1991, coll. D. Black (MV); 1♂, Otway Range, Young Ck Rd, 0.2 km NE of Ciancio Ck crossing, 38°40′S, 143°29′E, 420 m, 3.i.1995, coll. G. Milledge (MV); 1♀, Aire Crossing Tk, 0.5 km N of Aire R. crossing, 38°40′S, 143°29′E, 420 m, 31.i.1995, coll. G. Milledge (MV); 1♂, 1♀, Otway Range, Aire Ck site, 2.xi.1977, coll. P. J. M. Greenslade (SAM); 1♂, Otway Range, Blanket Bay, 38°49′S,143°43′E, 28.xi.1949, coll. P. Hoggart (MV); 1♀, Cape Otway, 38°51′S,143°32′E, coll. Mr Dixon (MV).


A
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Diagnosis

Papillae surrounding anal opening tan. Male head papillae not modified. Papillar scales ribbed in both sexes. Crural papillae on oncopods 2–14 (with papillae redueed on oneopods 4 and 5), or 2–3 and 6–14; all erural papillae blunt distally. Anterior aeeessory gland foramen U-shaped.

Description

Measurements. HWE males 0.87–1.12–1.38 mm (n = 11, holotype 1.25 mm HWE); females 1.25–1.51–1.90 mm (n = 11).

Color pattern (Fig. 14D). Ground-eolor greyish-blue, tan, or brown; primary papillae light-colored basally, dark tipped. Series of joined diamonds along midline, lateral angles in line with oneopods (ean appear sealloped in distended speeimens); diamonds lighter-eolored than surrounding integument and usually bordered by darker pigment (sometimes with pale tan papilla at lateral margin of eaeh diamond); laterally with longitudinal light-eolored band dorsal to oncopods and with light-eolored patches dorsal to oneopods. Papillae around anal opening tan. Ventral pigment present; ventral organs pale. Oneopods paler than body. Spinous pads pale yellow, or greyish-blue. Integument between genital and anal openings pigmented as for rest of ventrum.

Antennal rings. Banded, tan, or with tan mottle dorsally, or banded, tan or with tan mottle dorsally for half antennal length; dorsal banding on every fourth ring distal to and ineluding ring five, or on every eighth ring (or every sixth if very narrow rings not eounted). Greater than 30 antennal rings in adults; antennae with repeating pattern of wide, narrow, wide, very narrow rings; two rows of bristles on rings (eounting from distal to proximal) 3, 4, 6, 8 and 10; remaining rings with single row of bristles. Distal 9 antennal rings with sensory bulbs. Sensory pads with up to four rows of sensilla.

Eyes. EDI males 0.07–0.09–0.11; females 0.08–0.11–0.15.

Head (males). Males with no modifieation of head papillae (ie. papillae on head do not differ from remaining dorsal papillae) (some papillae fused, otherwise not modified) (Fig. 14E).

Head (females). Females with no modifieation of head papillae (Fig. 14F).

Integument. Males with 9–12–16, females with 15–17–25 papillae eounted from mid-dorsal line to junetion of oneopod 10. Dorsal body papillae not uniform size; alternate plicae with slightly larger primary papillae; dorsal primary papillae semieireular; papillar seales ribbed both sexes (Fig. 16A, B); lateral primary papillae slightly enlarged or elongate, with more prominent pair between oneopods in line with junetion of oneopods and body; papillae not reduced around anal opening.

Oncopods. Two bristles on anterior and posterior distal foot papillae, one bristle on median foot papillae.

Male reproductive tract. Proximal vasa efferentia lying elose together, parallel for part of their length before fusing to form vas deferens; vas deferens continues anteriorly from paired vasa efferentia for short distanee only before looping posteriorly toward gonopore (Fig. 16C, D).

Male glands and gland papillae. Crural papillae present on ventral side of oneopods 2–14 or 2–3 and 6–14 (if present on oneopods 4 and/or 5, erural papillae greatly redueed); erural papillae protrude between plieae 6–7 (eounting from third spinous pad). Papillae similar in shape on all oncopods: semieireular or eylindrieal proximally, tapered slightly distally, not divided into distinet basal and distal regions; with finely ribbed seales basally, distally seales with distinet ribs; smooth region surrounding distal foramen ovoid or lip-shaped,

Fig. 15. Ooperipatus porcatus, sp. nov.: A, head, holotype male, 1.30 mm HWE, scale bar 0.30 mm. B, primary papilla, paratype male, 1.25 mm HWE, scale bar 0.02 mm. C, male reproductive tract and associated glands, paratype, 1.25 mm HWE, scale bar 1 mm (aag, anterior accessory gland; cg, crural gland; pa, posterior accessory gland; sv, seminal vesicle; t, testis; vd, vas deferens; ve, vas efferens). D, crural papillae oncopod 2, paratype male 1.12 mm HWE, scale bar 0.04 mm. E, crural papilla oncopod 7, paratype male 1.25 mm HWE, scale bar 0.04 mm. F, crural papilla oncopod 7, side view, paratype male 1.12 mm HWE, scale bar 0.04 mm. G, crural papilla oncopod 12, paratype male 1.12 mm HWE, scale bar 0.04 mm.

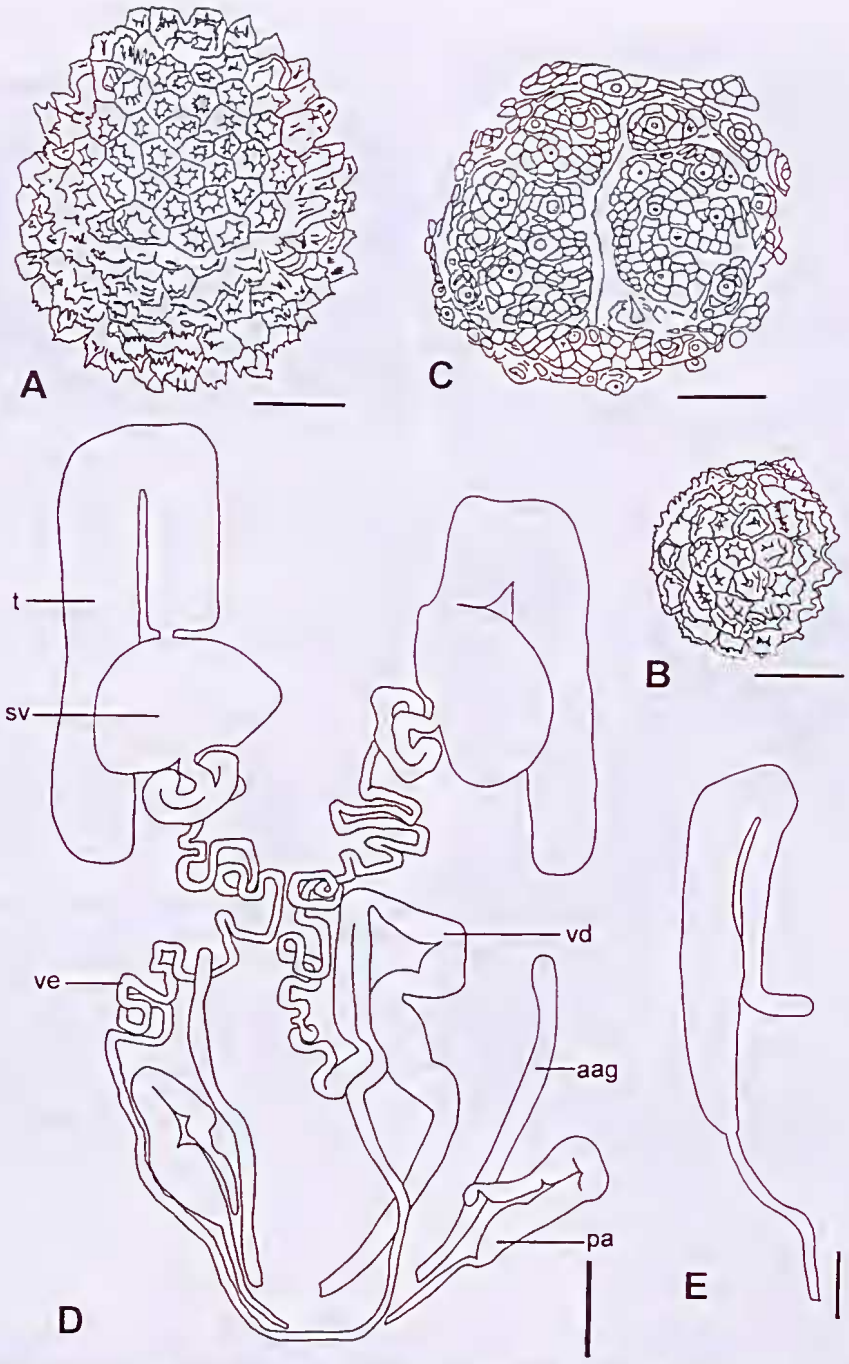

Fig. 16. Ooperipatus silvanus, sp. nov.: A, primary papilla, female, 1.45 mm HWE, scale bar 0.03 mm. B, secondary papilla, female, 1.45 mm HWE, scale bar 0.03 mm. C, genital pad, male, 1 mm HWE, scale bar 0.50 mm. D, male reproductive tract and associated glands, 1.15 mm HWE, scale bar 0.40 mm, crural glands not shown (aag, anterior accessory gland; pa, posterior accessory gland; sv, seminal vesicle; t, testis; vd, vas deferens; ve, vas efferens). E, posterior accessory gland, male 1.12 mm HWE, scale bar 0.30 mm.

not extending to papillar margin. Glands extend into lateral haemoeoel from oneopods 11–13; straight, short, not folded; remaining glands confined within oneopods. Anterior aecessory gland papillae large, semieireular; foramen a U-shaped slit. Anterior aeeessory glands long; lying freely within periviseeral haemoeoel; extending anteriorly approximately to oncopods 12–13; contents opaque, orange. Posterior aeeessory gland foramen open approximately midway between genital and anal openings; gland foramen separate, elose together; folded distally, long hook tapered only slightly to blunt tip (Fig. 16E).

Remarks

Ooperipatus silvanus, like *O. caesius* and *O. nebulosus*, does not have modified head papillae in males. Differenees among these three speeies are given in the *Remarks* section of *O. nebulosus*. Differenees between *O. silvanus* and other *Ooperipatus* are shown in Table 2. Females colleeted in Oetober, November, Deeember and January eontained thick-walled eggs in the oviduets. The body pattern may be indistinet in dark speeimens. This speeies has been found with an undeseribed *Ooperipatellus*.

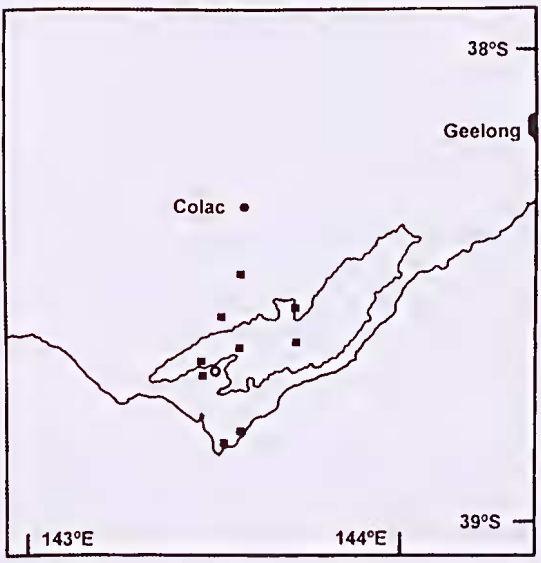

Fig. 17. Distribution of *Ooperipatus silvanus*, sp. nov. (solid squares, type locality, open circle). 300 m contour shown. See Fig. 6B for larger scale map indicating region shown here.

Habitat

In leaf litter and moss in eucalypt and *Nothofagus cunninghamii* forests. Speeimens were also found in and under logs and below tree ferns.

Distribution

Victoria, Otway Ranges, Gelibrand, 38°31′S,143° 32′E—Cape Otway, 38°51′S,143°32′E (Fig. 17).

Etymology

This speeies is named from the Latin, *Silvanus*, meaning 'the god of woods'.

ACKNOWLEDGEMENTS

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